PHYSIOLOGY OF FARM ANIMALS

BY

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PART I. GENERAL

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PREFACE

THIS book is addressed primarily to students of agriculture who may wish to obtain some knowledge of the simpler physiological processes as they occur in farm animals. It is hoped that it may be of use also to veterinary students. The second volume, by Professor Wood, dealing with animal nutrition, will be published shortly.

I take this opportunity of expressing my indebtedness to all those who have co-operated with me. Professor Wood has kindly read the proof sheets and made various useful suggestions. Mr E. T. Halnan, besides contributing the chapter on the sense organs, has also read the proof sheets and given me the benefit of his criticism; moreover, all those drawings which are new are the work of his hand. Mr R. H. Adie and Lieut-Colonel W. A. Wood have read the chapter on the locomotor organs and given me the advantage of their special knowledge. I wish to offer my grateful thanks also to those authors and publishers who have allowed me to reproduce illustrations from other works; in particular I desire to mention Sir Edward Sharpey Schafer and Messrs Longmans, Green and Co. I am under much obligation to Major-General F. Smith for the use I have made of his Manual of Veterinary Physiology, published by Messrs Baillière, Tindall, Cox and Co. Lastly I wish to thank my friend and colleague, Mr K. J. J. Mackenzie, for his constant encouragement and kindly interest, and for the ready help which he has always placed at my disposal.

F. H. A. M.

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CHAPTER I

INTRODUCTION

Physiology is the branch of science which is concerned with the *functions performed by living things*. It is a department of Biology or the science of life. But just as Biology is divisible into Botany which treats of plants, and Zoology which deals with animals, so there are also a Vegetable Physiology and an Animal Physiology, and it is the latter of these which forms the basis of medical and veterinary knowledge. For Physiology is the science which teaches us the way in which the body is built up, and how each part of it works, and the laws which govern its activities. In so doing it helps us to regulate these activities, and by teaching us about the normal working of the body, it shows us how any of its parts may be adjusted when they are out of order. This statement applies to the bodies of animals as well as to those of ourselves.

The present volume deals especially with the Physiology of the *domestic animals*. This is a branch of the subject which has been much neglected, for notwithstanding the great industrial importance of stock breeding and rearing, it is a business to which physiological science has been applied but little.

Like Chemistry and Physics, Physiology is founded on observations and experiments. These can sometimes be carried out upon ourselves, but are more often made upon animals. By means of a clinical thermometer we can perform a series of observations upon our own bodily temperature, establishing the fact that under normal conditions our temperature remains constant and is independent of that of the outside air which is usually considerably cooler. In this way we can learn a little about the fundamental nature of the organism, since we are led to perceive that our bodies like those of other animals must be supplied with the sources of that form of energy which we recognise as bodily heat. By extending our observations, and noting the increased blood supply of the skin and the tendency to sweat when we feel warm, we learn something

about the heat regulating mechanism which we possess in common with other warm-blooded animals. Again, by taking advantage of the fact that all the parts of an animal do not die at the same time we can perform a great variety of experiments which teach us much about the functions of the different organs of the body. Thus the excised limb muscle of a frog if kept moist by a saline solution, or the heart of a mammal if perfused with an artificial fluid resembling blood serum and preserved at body temperature, may be induced to survive many hours after the death of the animals from which they were taken, and from experiments upon these it is possible to learn much concerning the mechanisms of muscular contraction and the heart beat. Furthermore, we can carry out experiments upon entire animals, pain being avoided by the administration of anaesthetics during the progress of the operation.

Many of the functions of the body are essentially similar throughout the whole animal kingdom, and among Vertebrates there is a still closer likeness. Thus the processes of digestion in a frog, a bird, a rabbit, a horse, and a man are broadly speaking similar, though there are of course very marked differences which are generally greater the less closely related the animals are. So also the general laws governing the nature of nerve impulses, the movements of the heart, or the processes of reproduction are identical in every case. Thus by investigating any of these processes in a frog or in a rabbit, for example, we can learn a great deal about the functional activities of a horse, or a sheep, or a cow; and it is desirable that before specialising upon the Physiology of farm animals we should possess a general knowledge of the principles of the science obtained by studying whatever animals are most convenient for this purpose.

Furthermore, Physiology must always be studied in close relation to Anatomy or Morphology (that is, the department of Biology which deals with the form and structure of organisms), since it is impossible to acquire an insight into the functions of the various parts of an organism without possessing some knowledge of the composition and structural relation of those parts; and conversely, an intelligent comprehension of the form and structure of an organ can only be gained by a consideration of the part which that organ plays in the general economy of the individual.

The physical basis of all life, both vegetable and animal, is called protoplasm. The vital substance forming the most highly developed animals differs in degree rather than in kind from the undifferentiated protoplasmic mass composing the most simple form of life known. Protoplasm is a semi-fluid, transparent, viscous substance, which occurs usually in small individual particles, called cells. Sometimes it seems to be quite homogeneous but more often a reticulated structure can be detected. A study of its composition reveals that its most abundant constituent is water, which amounts to 75 per cent. of the whole material. The remaining 25 per cent. is made up of solids which consist chiefly of nitrogenous compounds called proteins, but certain metals (potassium and calcium) as well as phosphorus and sulphur are also present in a combined form together with small quantities of fats and carbohydrates.

An elementary knowledge of the physiology of protoplasm may be gained by studying the vital manifestations of the

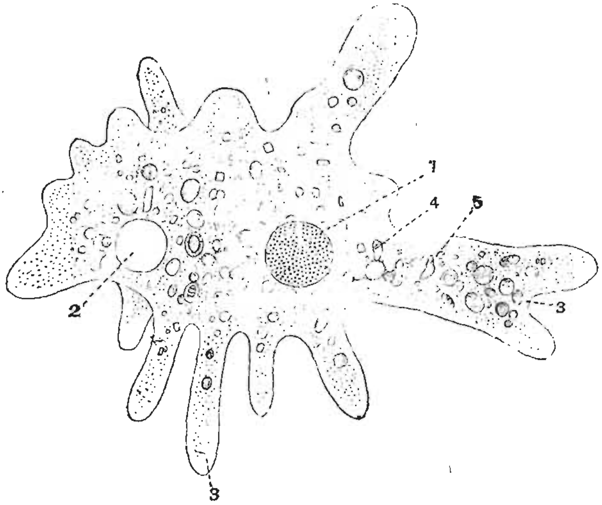


Fig. 1. Amoeba (after Graves, from Shipley and MacBride). 1 Nucleus, 2 Contractile vacuole through which waste products are excreted, 3 Pseudopodia, 4 Vacuoles containing food, 5 Grains of sand.

amoeba. This is a minute organism found in stagnant water, and resembling, when seen under the microscope, a little lump of moving jelly. It can be observed to move about spontaneously,

to eat up little particles of food, to excrete or get rid of waste products, to grow in size, and lastly, at a certain stage in its life-history, to reproduce by undergoing a process of simple division into two. In order to perform these functions it is essential that it should receive a supply of food, in just the same way as an engine cannot be made to work unless it is provided with fuel. In the latter case the fuel undergoes combustion which liberates heat. So also in the case of the animal the energy is derived from the complex food material, which undergoes a process of slow oxidation, thereby breaking down into simpler substances and setting free the energy necessary for the discharge of the vital functions. The changes which the food or its constituents undergo in the amoeba or any other organism are classed together under the term 'metabolism': those of them which relate to the building up of the food into the material of the body are referred to as 'anabolic' or 'assimilative'; while the changes which are associated with activity, resulting from a breaking down of complex substances into more simple ones, are known as 'katabolic' or 'dissimilative.'

An amoeba consists of a single cell, that is to say, a minute mass of protoplasm containing within it a certain specialised portion known as the nucleus which can generally be readily identified under the microscope by its more intense staining capacity. The nucleus is essential to the life of the cell. There are many different kinds of unicellular organisms, varying in form but all resembling the amoeba in their general plan. Higher in the scale we find groups of amoeba-like cells, each with their nucleus, aggregated together with little or no division of function. Such an arrangement occurs in the simpler kinds of sponges. But in the majority of multicellular animals whole groups of cells are separated off to subserve particular functions; and these form the various tissues. The body of a higher animal is, however, derived from a single cell essentially similar to that of an amoeba, and this, in the process of individual development, undergoes a long series of divisions in the progress of which the nuclei also divide. The products of division, that is to say, the cells with their contained nuclei, become gradually specialised to form the different tissues—bone, cartilage, muscle, nerve, connective tissue, etc. Thus the outer layer of cells becomes adapted for protection and for receiving the impressions produced by

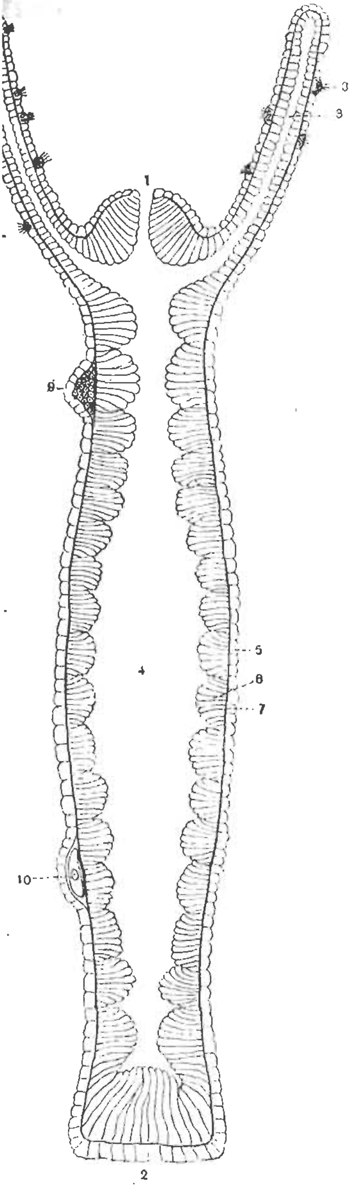


Fig. 2. Diagrammatic longitudinal section through *Hydra*, a tubular animal showing cellular differentiation of a simple kind. (From Shipley and MacBride.) 1 Mouth, 2 Foot, 3 Tentacle, 4 Digestive Cavity, 5 Outer layer of cells or Ectoderm, 6 Inner layer of cells or Endoderm, 7 Structureless jelly between the two latter, 8 Groups of cells specialised for offensive purposes and containing structures which can be ejected, 9 Testis, 10 Ovary.

changes in the surroundings; the inner layer lining the gut becomes adapted for the digestion and assimilation of food; while between these are developed the skeleton and general framework of the body, and all the other tissues which assist in performing the vital functions.

These functions may now be considered more closely. The parts concerned with each function are usually called systems, and the subsidiary parts which compose these systems are known as organs. The following are the principal systems of the body in a higher animal: (1) the digestive system; (2) the circulatory system; (3) the respiratory system; (4) the excretory system; (5) the muscular system; (6) the nervous system; and (7) the reproductive system. In addition to these are the organs of special sense, such as the eye and ear, and the various organs of internal secretion.

Digestive System. In such lowly forms of life as the amoeba, food is taken in at any point on the surface, and is then assimilated, the indigestible residue being cast out at some other part of the surface. But in man and in all the other higher animals there is a differentiation of function, food being taken in only at a definitely located mouth, whence it passes down an alimentary canal which is divided into several portions. In some of these the digestible material is absorbed, passing through the wall of the canal and into the neighbouring lymph vessels or blood vessels, whence it is distributed throughout the body. The indigestible residue is expelled at a definite anus, which is placed at the hind end of the body. The actual digestive process takes place through the action of various glands such as the salivary glands, the gastric glands, the liver and the pancreas, all of which pour out juices having a digestive or solvent action on the food stuffs.

Circulatory System. To enable the food which is absorbed from the alimentary canal to be distributed to all the organs of the body a circulatory medium is provided, and this medium is the blood. In all higher animals the blood is kept in motion by a central organ of propulsion, the heart. In a mammal the heart is divided into four chambers—a right and a left auricle, and a right and a left ventricle. Each chamber communicates with the adjoining ones by valves, which only permit of the blood passing in one direction. The circulation is maintained by

the heart alternately contracting and dilating, the compressing force being supplied by the muscular wall of the organ. The heart communicates with an elaborate system of vessels, those which carry the blood away from it being called arteries, while those which bring the blood back are called veins. The arteries possess thicker and more elastic walls than the veins. The arteries become divided up in the peripheral parts of the body into a number of much smaller vessels, the capillaries, which permeate the tissues. Some of the fluid of the blood transudes through the walls of these vessels, becoming the lymph and bathes the cells with blood. The capillaries unite again to form the veins, which transport the blood back to the heart. If the web of a living frog's foot be examined under the microscope, the circulation of the blood in the capillaries may be observed quite easily.

The red colour of blood is due to the presence of innumerable little red disks known as corpuscles, which float in a yellowish-coloured semi-transparent fluid, the blood plasma. In addition to these red corpuscles, blood also contains a relatively small number of white corpuscles or leucocytes, which have the power of independent movement and resemble the unicellular amoebae referred to above. One of their functions is to eat up and so destroy the germs of disease.

As already mentioned some of the products of digestion are absorbed into vessels containing lymph which is a colourless fluid resembling blood plasma. The lymph vessels or lymphatics communicate with veins so that the substances present in lymph eventually enter the blood system.

Respiratory System. In order to keep an animal alive it is necessary to supply it with oxygen, for, as we have seen, every animal is dependent for its source of energy upon the slow oxidation of the material which it builds up out of its food supply. As a result of this oxidation process it is continually giving off carbon dioxide. In the higher vertebrates the organs which are concerned in this gaseous exchange are the lungs; but in the lower forms of life the entire surfaces of the body serve to effect the interchange of oxygen and carbon dioxide; while in many other animals, which live in water (e.g. fishes), the respiratory organs take the form of gills.

The lungs of an animal are connected with the exterior by

the windpipe or trachea, which opens into the back of the mouth at the root of the tongue. This tube at its lower end divides into the two bronchi, and these subdivide again and again within the lungs like the branches of a tree. Their finest divisions widen out into air sacs which are in close relation to a meshwork of capillaries, the air in the air sacs and the blood in the vessels being separated from one another by only a very thin layer of protoplasm. These air sacs and capillaries form an essential part of the structure of the lungs. Here the gaseous exchange is effected, the blood taking up oxygen from the air sacs and giving off carbon dioxide. When the blood passes to the tissues this process is reversed, the carbon dioxide being taken up from the tissue cells, while oxygen is given off to these cells. The arterial blood, or blood which is being circulated to the tissues after having been to the lungs and heart, is bright-red in colour owing to the presence of a compound called oxyhaemoglobin, which contains oxygen in loose combination: whereas venous blood which is in process of being returned to the heart and lungs is purple, the oxyhaemoglobin having been reduced, in part at least, to haemoglobin, thereby causing a change in the colour of the corpuscles. The complete course of the circulation in a mammal is as follows: Right auricle of heart, right ventricle, pulmonary arteries, lungs, pulmonary veins, left auricle, left ventricle, arteries (excepting pulmonary arteries), capillaries, veins (excepting pulmonary veins), and so back to the heart.

The interchange of gases which takes place between the lungs and the external air is effected by the alternate expansion and contraction of the chest wall, the air passing through the windpipe in opposite directions in the acts of inspiration and expiration. In this way the excess of carbon dioxide in the lungs is got rid of, and a supply of oxygen from the external air is able to take its place

Excretory System. We have seen that the protoplasm of which an animal is composed consists principally of protein. This consists of carbon, hydrogen, oxygen, nitrogen, and sulphur. As a result of katabolism these elements must be got rid of. A great part of the waste carbon and oxygen is disposed of by the lungs in the form of carbon dioxide as just described. The hydrogen and a further proportion of oxygen are excreted in the form of water vapour both through the lungs and the

skin. The waste nitrogen, however, and also the waste sulphur (but this is only a small amount, since sulphur is present in only small quantity in protoplasm) are got rid of for the most part by the kidneys, which are commonly described as excretory organs. For just as the cells of the body discharge their waste carbon dioxide into the blood, so also do they dispose of their nitrogenous products, and these are carried to the kidneys. In the latter the blood capillaries are separated by only a single cellular layer from the cavity which communicates with the exterior. The cells of this layer absorb the waste products and excrete them into the kidney tubules, together with water and some salts in solution. These form the urine, which flows down a duct termed the ureter into the bladder, from which it is expelled at intervals to the exterior in the act of micturition.

Muscular System. A muscle is an especially contractile organ which is either circular (as in sphincter muscles) or straight. The latter is the more usual form among the higher animals. Such a muscle, upon contracting, reduces the length between its two farthest points. One of these points is usually called the origin of the muscle and the other its insertion. The muscles are attached to bones, and these by their movements may become inclined to one another at various angles. In the case of the limbs these angles are opened and closed, thereby causing progression, and the mechanical aid which is introduced to effect this is that of the lever. The muscles themselves are fleshy masses composed of fibres. Some muscles, such as those of the limbs, are under the direct control of the will and are consequently often called voluntary muscles; whereas others like the muscles surrounding the intestines, which are not under the control of the will, are termed involuntary muscles. The voluntary muscles form a considerable part of the body, and constitute the flesh or meat on an animal. Broadly speaking, the muscular system is that part of the body in which the energy set free by the oxidation of the food material is converted into motion and so carries on work.

Nervous System and Sense Organs. In the lowest forms of animal life the protoplasm is uniformly irritable and contractile; but in the higher types, as just shown, the organs of movement are concentrated in a motor or muscular system, while there are also definite organs of sense (eye, ear, etc.). Such division of

labour necessitates a means of communication between the various organs, and this function is fulfilled by the nervous system. The nerves consist of strands of a peculiar kind of tissue constituting the nerve fibres, and these connect together the sense organs and muscles and all the various parts of the body. The nervous system is presided over by the brain and spinal cord. The former of these is contained within the skull, while the latter consists of a hollow tube enclosed by the backbone or vertebral column. The brain and spinal cord together constitute the central nervous system. The other nerves are differentiated into afferent (sometimes called sensory) nerves, in which the impulses pass from the sense organs to the central nervous system, and efferent (sometimes called motor) nerves, in which the impulses travel outwards from the central nervous system to the muscles or other organs to which a message is to be sent. All actions which are under the control of the will are presided over by the brain, from which the voluntary nervous impulses are transmitted. But there is another class of actions in which either the brain or spinal cord is concerned, but which are involuntary. These are called reflex actions. For example, if a frog after being deprived of its brain be hung up by its jaw and one of its toes pinched, its leg is drawn up. Such an act is involuntary, and in this case is controlled by that part of the central nervous system which is still intact, namely the spinal cord. If this be destroyed the reflex action can no longer take place. It is clear, therefore, that such an act involves a succession of processes, which are as follows. The pinching of the toe supplies a stimulus which is transmitted as a nerve impulse by an afferent nerve to the spinal cord. Another nerve impulse is then transmitted by an efferent nerve in the opposite direction, passing from the spinal cord to the muscles of the limb, and this causes them to contract. There are also cerebral reflexes, which are likewise involuntary. For example, the secretion of the saliva and the secretion of the gastric juice are reflexes which are induced by the introduction of food into the mouth, messages being transmitted in the first place in an afferent direction from the mouth to the brain, and then in an efferent direction from the brain to the secretory glands of the mouth and stomach. It is interesting to note that different sets of nerves are concerned in transmitting the impulses in opposite directions. Every reflex

is presided over by a special centre in the central nervous system, these centres being the parts of the brain and spinal cord that receive the afferent impulses and dispatch the efferent ones which are concerned in the reflexes in question. In the body of a higher animal a close succession of reflex actions is continually going on, and it is in this way that the individual organism is able to react to environmental changes, and so fit itself to its surroundings.

Reproductive System. In the unicellular organisms like the amoeba, reproduction is carried on by simple cell division. In the higher animals, however, there are certain special cells set apart for reproduction, the ova in the female and the spermatozoa in the male. The ova and spermatozoa are produced respectively in the ovaries and testicles. Their function is to unite together, a single ovum fusing with a single spermatozoon and giving rise to a conjugated cell or oosperm, which by a long succession of cell divisions develops into a new individual. In each of these divisions the cell nuclei also divide so that each product of division always contains a nucleus. In the mammal the development of the unborn young takes place in a special organ, the uterus, 'womb' or 'bed' whence they are expelled in the act of parturition or giving birth.

Organs of Internal Secretion. In addition to the various systems described above, we find also certain organs that have the power developed to a special degree of altering the composition of the blood by secreting into it chemical substances which are elaborated for the advantage of other parts of the body, whither they are conveyed in the blood stream. Many of the organs referred to above which subserve the functions already mentioned are in addition internally secreting glands, thus fulfilling more than one purpose. Such organs are the liver, the pancreas, the ovary, and the testicle. The liver, besides secreting bile, stores up a supply of carbohydrate in the form of glycogen, and when required liberates it into the blood as sugar. The pancreas also in some unknown way controls the carbohydrate metabolism, since after its experimental removal sugar makes its appearance in the urine, thereby indicating an excess of sugar in the blood. But there are certain other organs, which appear to be solely organs of internal secretion. Such are the suprarenal bodies, which are situated just in front of the kidneys, one

on either side. These secrete into the blood a substance known as adrenalin, which acts on the muscles, particularly those of the blood vessels. If these organs are removed extreme weakness, associated with muscular collapse, results, and is followed sooner or later by death.

CHAPTER II

HISTOLOGY

Histology is the study of the minute structure of the tissues of the body. Since it is carried out by means of the microscope it has been described as Microscopic Anatomy.

The tissues of which the different organs are composed may be divided into four main groups as follows:

(1) Epithelial tissues.
(2) Connective tissues.
(3) Muscular tissues
(4) Nervous tissues.

(1) **Epithelial Tissues.**

An *epithelium* may be defined as a cellular membrane bounding a free surface. There is a certain amount of cementing substance present between the cells, but this is reduced to minimal proportions. There are two main kinds of epithelia, simple and compound.

In *simple epithelia* the cells form one layer only. They may be cubical in shape like those lining the tubules of certain glands such as the pancreas, or columnar like some of the cells lining

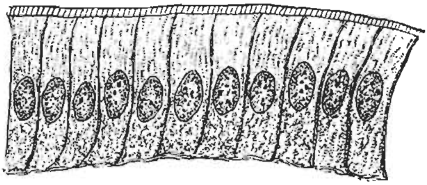


Fig. 3. Columnar epithelium from intestinal villus (from Gray).

the inside of the stomach or intestine. They may be provided with cilia or fine filaments, as with the cells of the uterus, in which case we speak of a ciliated epithelium. Moreover the lining membrane may consist of a layer of thin cells arranged in the

manner of flat paving-stones closely fitted together such as we find surrounding the air sacs of the lungs. Such a tissue is described as a pavement epithelium.

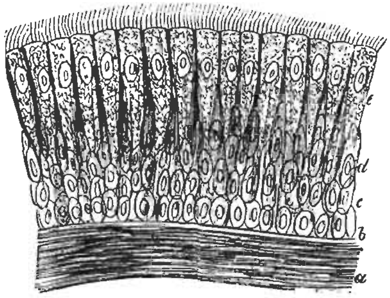


Fig. 4. Ciliated epithelium from trachea (from Gray). *a* elastic fibres within, *b*, *c*, *d* epithelial cells of mucous membrane, *e* ciliated epithelial cells.

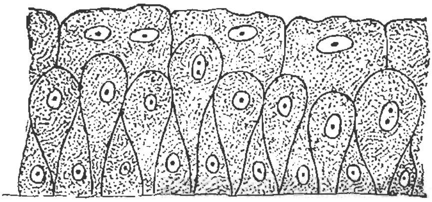


Fig. 5. Transitional epithelium (from Gray).

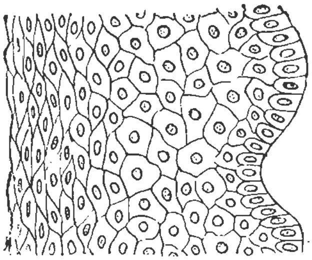


Fig. 6. Stratified epithelium from oesophagus (from Gray).

In *compound epithelia* the tissue consists of more than one layer of cells. When the cells are arranged in two, three or four superimposed layers the epithelium is frequently called transitional, but if the number of layers is considerable, we speak of a stratified epithelium. The tissue lining the urinary bladder is

a transitional epithelium; that forming the epidermis or superficial portion of the skin is a stratified epithelium. In addition to these kinds of epithelia there are the more specialised forms

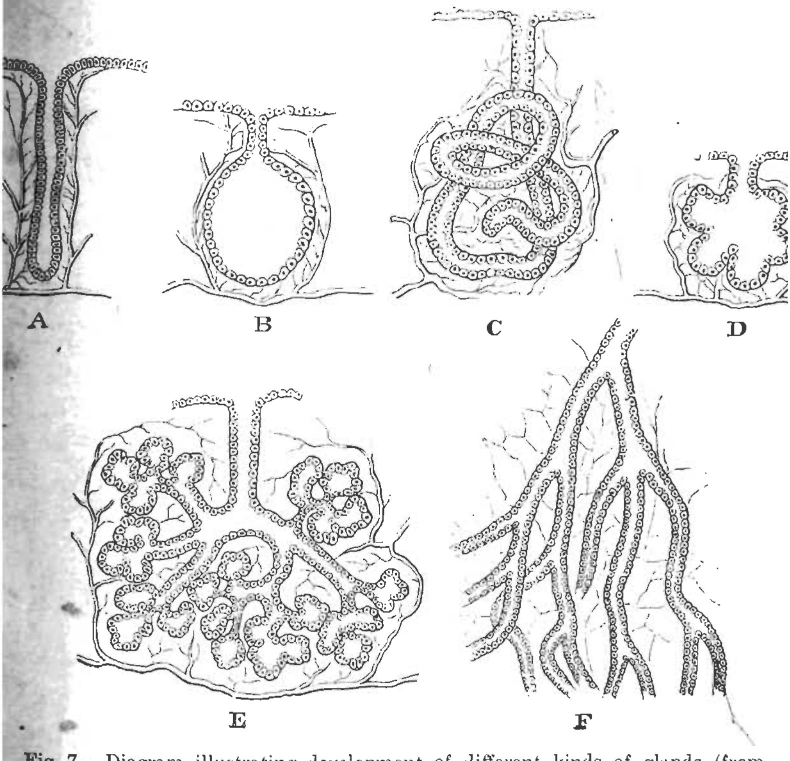


Fig. 7. Diagram illustrating development of different kinds of glands (from Gray). *A* simple gland, *B* sacculated gland, *C* convoluted tubular gland, *D* and *E* racemose glands, *F* compound tubular gland.

present in secreting glands, and certain sense organs, besides those structures like horn, tooth enamel, etc. which are of the nature of modified epithelia. These are described later in dealing with the physiology of the organs concerned.

(2) **Connective Tissues.**

The connective tissues are found throughout the whole body lying between and binding together the different organs or parts of the same organ. Their function is to act in a purely mechanical manner giving support where required and at the same time

admitting of the necessary amount of elasticity or rigidity. In embryonic development they have an identical origin, and there are all gradations between the various kinds of connective tissue. They agree further in having a large amount of intercellular cementing substance, and in this substance fibres are developed. Although situated outside of the cells this intercellular substance in the first instance was derived from the cells.

One of the commonest kinds of connective tissue is called *areolar tissue*, which is found in great abundance just under the skin. It consists largely of a close meshwork formed of bundles of fibres which are white in colour and very fine and wavy.

Fig. 8. Areolar tissue (after Szymonovicz from Halliburton). 1 branched cell, 2 white blood corpuscle emigrated from a neighbouring vessel, 3 elastic fibres, 4 white fibres.

Elastic fibres are also present. These are generally thicker than the white fibres; they are yellowish in colour, and as a rule much straighter. In addition to the fibres there is a clear ground substance containing several kinds of cells which can be seen lying amid the fibres. The cells, which contain easily discernible nuclei, are in many cases flattened and branched, but there are other kinds of cells which resemble or are identical with some of the white corpuscles of the blood.

Fibrous tissue which we find in tendon or sinew is almost wholly composed of white fibres. In *elastic tissue* which occurs in ligaments as well as in the lungs and the walls of the blood vessels elastic fibres are the chief constituent. Otherwise both these kinds of connective tissue resemble areolar tissue.

Cartilage, commonly called gristle, is a modified form of fibrous

tissue, which occurs at the ends of bones where these take part in forming joints. It is firm, and at the same time elastic and to a certain extent yielding so that it saves the bones from the

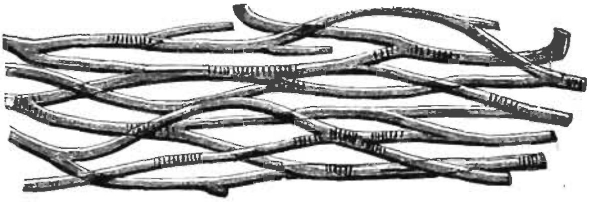


Fig. 9. Elastic fibres (from Schafer).

effects of concussion and the body from the jar which would otherwise result. It occurs also in the wall of the windpipe, in the nostril, and in the external ear, besides supplying firm but elastic connections between the vertebrae, and between the ribs and the sternum. Moreover, most of the bones are first laid down in embryonic development as cartilage and only become ossified in later life.

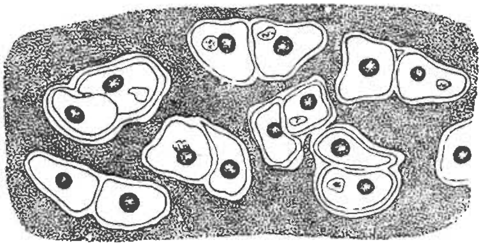


Fig. 10. Hyaline cartilage (from Gray).

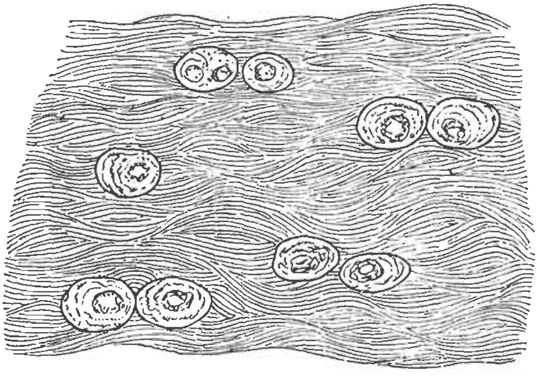


Fig. 11. Fibro-cartilage (from Gray).

All cartilage consists of a matrix or ground substance containing cells scattered within it. There are three principal kinds of cartilage, *hyaline cartilage* in which the matrix is almost clear and transparent, *white fibro-cartilage* in which the matrix contains white fibres, and *elastic fibro-cartilage* in which elastic fibres are present.

Bone is a form of tissue produced by the ossification of connective tissue. It may be divided into two classes according to its origin, cartilage bone and membrane bone. Bone of the latter kind is formed by the deposition of lime salts in the ground substance of embryonic connective tissue. In this way such bones as the maxillary bone are produced. Cartilage bones

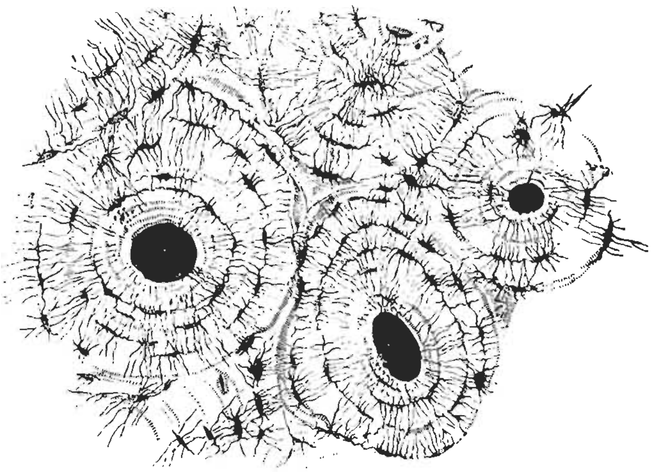


Fig. 12. Compact tissue of bone (after Sharpey from Gray).

(e.g. the limb bones) are formed through the activity of the cartilage cells. These become enlarged and arranged in rows, and give rise to fibrous lamellae which afterwards undergo calcification. The tissue becomes excavated by small holes through which blood vessels, arising from the periosteum or covering vascular membrane, pass into and through the bone. A fully formed bone is seen to be composed of lamellae, consisting of fine fibres which are calcified, lying in a matrix which is also calcified, and contains the bone corpuscles or cells of the tissue. Bone may be either compact as in the shaft of a long bone (e.g. the femur) or cancellous as in the ends of such a bone. In com-

pact bone the blood vessels are contained in little canals—the Haversian canals—which are very numerous throughout the bone; in cancellated bone the vessels run in the interstices into which the bone marrow extends. The marrow is contained chiefly in the hollow cavity which extends throughout the length of the shaft but is not continued into the enlarged ends. The marrow consists largely of fat, but often contains a considerable amount of blood, which then gives it a characteristic red colour.

Reticular tissue also occurs in bone marrow, as well as in the liver, spleen, lymphatic glands, and various other parts of the body. It is essentially a connective tissue in which the intercellular substance has partly disappeared or been replaced by fluid, but it contains white fibres, and sometimes elastic fibres.

Lymphoid tissue may be described as reticular tissue or areolar tissue in which the meshes are packed with large numbers of small round cells called lymphocytes or lymph corpuscles. It occurs in the spleen, tonsils, and thymus, and in all lymphatic glands. (For figures of spleen and thymus see pages 148–9.)

Adipose tissue is connective tissue containing a large proportion of fat in its cells. The fat globules are at first very small,

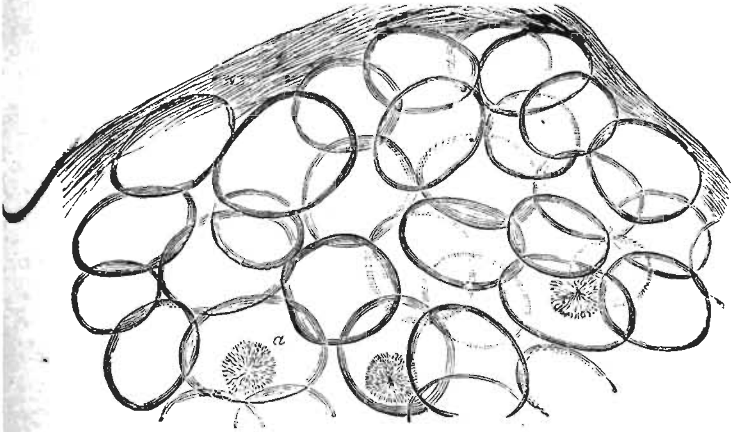


Fig. 13. Adipose tissue (after Gray). *a* crystals of fatty acids.

and then gradually increase in size so as to coalesce, pushing the cell protoplasm with its nucleus to the periphery or chiefly to one side, so that there comes to exist a single fat globule surrounded by a thin layer of cell substance a portion of which

contains the nucleus. Adipose tissue is found mainly just beneath the skin, and in other places where it serves as a packing, holding the organs in position and protecting them from injury. It helps to give the limbs their characteristic contour. It provides a store of nutriment for the bodily requirements, besides acting as a non-conductive layer under the skin, and so helping to retain the bodily heat. In fat animals adipose tissue occurs in great quantity in the abdominal cavity, especially in the region of the kidneys, as well as between the various muscles; sometimes also the muscles are themselves penetrated by fat, the flesh becoming marbled in appearance.

(3) **Muscular Tissues.**

Muscular tissue consists mainly of fibres in which all the primitive functions of the cell have become subservient to the function of contractility. There are three kinds of muscular tissues, which differ from one another both in their histological structure and in the functions which they perform.

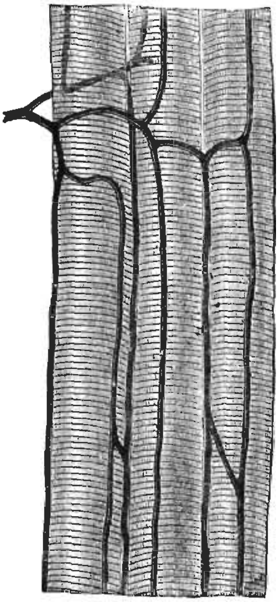


Fig. 14. Striated muscle showing capillary vessels (from Schafer).

In *voluntary* or *striated muscle* the fibres are long and cylindrical with characteristic cross striping, consisting of alternate dark and light bands. Each fibre has an elastic sheath, called the sarcolemma, which insulates the cells from one another and assists in forming the attachment of the muscle to the bone. In addition to the sarcolemma and striated substance, a muscle fibre has also a number of oval nuclei generally associated with a little undifferentiated cell protoplasm. This protoplasm, together with the interstitial substance between the elements composing the fibre, is the remains of the protoplasm of the cells which originally gave rise to the muscle fibres. Striated muscles are attached to the bones of the body and are under the control of the will; hence they are also

called skeletal muscles, or, as already mentioned, voluntary muscles.

Cardiac or heart muscle also shows a transverse striation, but the cells are short and squat, and have branches which unite

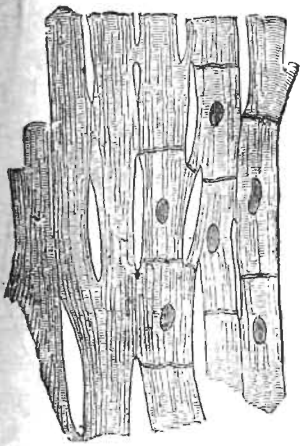


Fig. 15. Cardiac muscle (from Schafer).

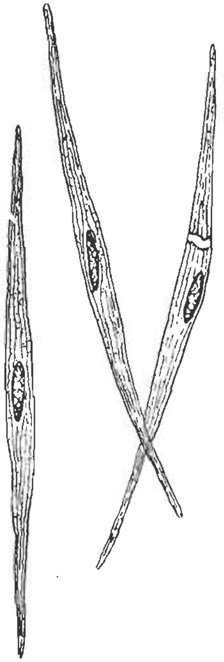


Fig. 16. Unstriated muscle fibres from bladder of frog (highly magnified). Note the spindle shaped nuclei and the longitudinal fibrillation.

them with those of neighbouring fibres, and there is no sarcolemma. Each cell has a central nucleus.

Involuntary, non-striated, smooth, or *plain muscle* is devoid of striations. The cells are usually fairly long and taper at both ends. The nucleus which is elongated is situated centrally. Connective tissue is present (as in the case of heart muscle) but there does not appear to be a true sarcolemma. Smooth muscle occurs in the walls of the alimentary canal, the trachea, the urinary bladder, the uterus, and various other organs, the movements of which are not under the control of the will. It is well developed also in the middle coats of arteries, veins, and

lymphatics, besides occurring in parts of the skin in association with sweat glands and hair follicles.

(4) **Nervous Tissues.**

The minute anatomy of the nervous tissues is most con-

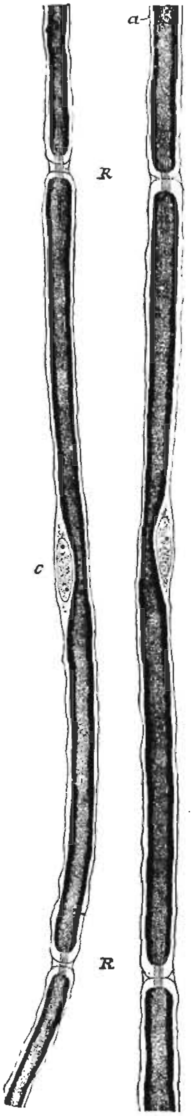


Fig. 17. Medullated nerve (after Neale, from Schafer) showing nodes of Ranvier, *R*, where medulla is broken, the axon passing through. *a* Neurolemma outside of medulla, *c* nucleus and protoplasm between primitive sheath and medulla.

veniently described in dealing with the nervous system. Here it will suffice to give a brief account of the different kinds of nerve fibres and the cells from which they arise.

If we cut across a nerve trunk, and examine a section of it under the microscope we find that it is made up of a large number of nerve fibres which are held together by connective tissue. If we confine our examination to one of these fibres we find that it consists of a central strand or core, known as the axis cylinder or axon, and an outer portion consisting of the medullary sheath and the neurolemma, the latter being a fine membrane which surrounds the sheath. The axon is concerned with the conduc-

Fig. 18. Non-medullated nerve fibres from Nissl preparation of vagus of cat (photograph from Schafer).

tion of the nerve impulse; the medulla, which is not quite complete but is broken at intervals, is of the nature of a protective covering and is composed of a phosphorised fatty substance. Such nerve fibres are called *medullated fibres*. Intermingled with these are other fibres in which the medullary sheath is lacking. These are called *non-medullated fibres*. They are especially common in the so-called sympathetic nerves. These non-medullated fibres appear to possess numerous nuclei, but the nuclei almost certainly belong actually to a very thin investing sheath.

If we follow a nerve fibre along its entire length we finally come, either in one direction or the other, to the nerve cell of which the axon of the fibre is in reality a part. For the nerve cells give off prolongations, sometimes a great many and sometimes only a few, and these prolongations become the axons of the nerve fibres. A nerve cell possesses a nucleus like all other cells and external protoplasm which contains characteristic fibrils and granules. The name *neuron* is applied to the nerve cell together with all its various prolongations, including the axons of the nerve fibres. (See fig. 46, p. 98.)

CHAPTER III

THE DIGESTIVE ORGANS

The substances which occur in an animal's food may be divided for our present purpose into the following main groups:

(1) Proteins which contain the five elements, carbon, oxygen, hydrogen, nitrogen, and sulphur combined together to form molecules of very large size. Albumen or egg-white, gluten found in wheat flour, casein found in milk, and myosin which is an important constituent of lean meat, are examples of proteins.

(2) Amides which like proteins are nitrogenous substances but of relatively simple composition. They are of little importance as constituents of food.

(3) Carbohydrates which are compounds of carbon, hydrogen, and oxygen, the two latter elements being always present in the same proportion as in water. Starch ($C_6H_{10}O_5$), grape sugar ($C_6H_{12}O_6$), cane sugar ($C_{12}H_{22}O_{11}$) and cellulose ($C_6H_{10}O_5$) are examples.

(4) Fats which contain the same elements as carbohydrates, but with the carbon and hydrogen in very great excess over the oxygen.

(5) Salts which though not strictly foods since they are not energy producers, are yet essential to the organism since they supply certain necessary elements. The chlorides and phosphates of sodium, potassium and calcium are examples.

(6) Water which though not a food is absolutely essential to the organism, being present in every living cell.

In the present chapter it is proposed to describe the organs which are concerned with digesting, or rendering fit for assimilation, the different classes of foods.

The relative importance of the food stuffs for the well-being of the animal is dealt with later in the volume on nutrition.

The Mouth. The organs employed by animals for conveying the food to the mouth are the lips, tongue, and teeth, but the precise part played by each varies in the different species. A horse when feeding in a manger for example, employs its lips

for collecting the food, and for this purpose they are strong and thick and are richly supplied with end organs or organs of touch. The lips are not used by a horse when grazing, but are drawn back so as to allow the incisor teeth to bite off the grass. In the ox the lips play a small part, but the tongue is used freely, being first protruded and curled round the grass, and then withdrawn into the mouth, while the grass is cut off between the incisor teeth of the lower jaw, and the dental pad which takes the place of the teeth in the upper jaw. In the sheep and goat the upper lip is divided into two parts each of which is possessed of independent movement. As in the ox the lower incisors bite against a pad in the upper jaw, there being no upper incisors. By reason of the cleft upper lip the sheep and the goat can bite more closely to the ground, and thus they can get a living where a horse or an ox could not do so. In all these animals the tongue is employed in pressing back the food to the hinder part of the mouth where it is brought under the action of the molar teeth. The tongue is assisted in most animals by grooves in the palate. In the ox there are papillae covering the inside of the mouth and inclining backwards. The object of these is believed to be to assist in preventing the food from falling out of the mouth.

The tongue differs considerably in the horse and the ox; in the former animal it is relatively smooth and swells out at the apex, in the latter it narrows from the base to the apex, being pointed; moreover it is very rough and well able to resist injury from coarse grasses. The movements of the tongue may be very extensive in the ox and the dog, but horses seldom protrude their tongues.

The process of mastication is very effectively carried out in all herbivorous animals, for the molar teeth, by reason of the hard enamel ridges separated by the softer cement substance, wear with a rough surface, and are admirably adapted for grinding and crushing the food

The lower incisor teeth in those animals in which there is a dental pad are placed obliquely in the jaw so that the pad is not injured when the mouth closes. For the same reason they are capable of free movements in their sockets. In the horse the incisors in both jaws are at first vertical, but become oblique with advancing age. All the teeth are gradually pushed out from their sockets, the fangs becoming reduced in length; at

the same time the teeth are ground down through wear and tear. By taking advantage of this fact the age of an animal can be determined after it has acquired its full mouth of permanent teeth. At an earlier period of life, the age can be ascertained by noting the number and arrangement of the temporary or milk teeth.

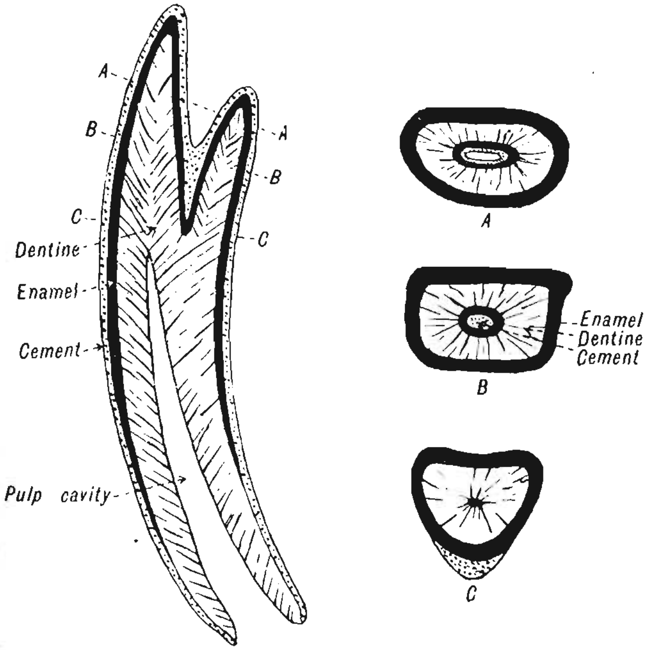


Fig. 19. Longitudinal and cross-sections of incisor tooth of horse. Cross sections A, B, C illustrate the surface appearance of the tooth at various stages of wear. Note that the peripheral cement quickly disappears from the newly erupted tooth in situations subject to wear.

The movements which the jaws undergo to admit of mastication vary somewhat in different animals. In the dog there is a simple up-and-down movement of the lower jaw, and for this purpose the articulation of the jaw is of the simplest kind. Hardly any effort is required for opening the mouth, for this movement merely involves a depression of the lower jaw, but powerful muscles are provided for closing the mouth, that is, for elevating the jaw. This statement applies to the horse and ox and other animals besides the dog, but the horse, ox and sheep differ from

the dog in being able to move the jaw laterally as well as up and down. Thus the articulation of the lower jaw in these animals is provided with a well-developed cartilaginous disc which is sufficiently yielding to admit of movement in different directions.

Mastication is very thoroughly performed in the horse, which may take as much as ten minutes to eat a pound of corn, or twenty minutes to eat a pound of hay. In ruminating animals mastication is performed principally after the cud has been returned to the mouth. In the dog the food is only very slightly masticated.

In the horse and ox and other herbivorous animals mastication only takes place on one side at a time. To facilitate this unilateral mastication the upper jaw is wider than the lower; otherwise the molar teeth would not properly meet during the process. A horse or an ox will masticate on one side only for many minutes at a time before transferring the food to the molars on the opposite side.

In drinking, the tongue is drawn backwards, while the lips are shut excepting for a small orifice in front which is placed under the surface of the water. The water is thus sucked in by the action of the tongue, the cheeks being drawn inwards at the same time. The act of sucking as performed by young animals is essentially similar, the size of the tongue being decreased in front and increased behind. A horse while drinking extends its head, moving its ears forwards during each swallow and letting them fall back in the intervals between the swallows. Lapping as performed by the dog and cat is carried out by the animal curling its tongue and using it like a spoon and so conveying the liquid into the mouth, the tongue being withdrawn and extended in a succession of rapid movements.

Deglutition or the act of swallowing occurs normally in three stages. In the first stage the food is carried back to the base of the tongue by the action of the tongue muscles. In the second stage the larynx is pulled upwards and its entrance closed by the pressure of the tongue on the cartilaginous epiglottis which guards the entrance to the windpipe. The posterior nares which communicate with the nostrils also become closed by muscular action, and the food is grasped by the muscles of the pharynx and forced into the oesophagus. In the third stage of swallowing the food is carried down the oesophagus by successive waves

of muscular contraction which pass through its entire length from the pharynx to the stomach. Swallowing is facilitated by the presence of saliva without which it can only be performed with difficulty. It can be performed against gravity since it is a definite muscular act, the peristaltic waves of contraction passing along the oesophagus altogether irrespectively of the position of the individual. In swallowing fluids the action is very rapid and may be carried on at the rate of one swallow every second.

The first act in the process of swallowing is voluntary, but the second and third acts are purely reflex, being presided over by a definite centre in the hind brain which is informed of the presence of food by afferent nerves coming from the pharynx. Impulses are then conveyed by efferent nerves passing to the different muscles concerned in swallowing. Afferent impulses may be started by touching the inside of the windpipe or the rim of the glottis and the swallowing centre will be thereby stimulated.

The oesophagus in the horse differs from that of the ox and most other mammals in one important respect. The thin red striated muscle, which surrounds it throughout the greater part of its length, gives place to thick, pale, non-striated muscle at its lower end, where it is tightly contracted, the lumen being very narrow. It is largely for this reason that horses experience such difficulty in vomiting. In the ox and sheep the muscles of the oesophageal wall are red and striated throughout, and the lumen of the organ is widely distended at the lower end, so as easily to admit of the food passing back into the mouth in the process of rumination.

The Salivary Glands. Just prior to and during mastication saliva is secreted in considerable quantities and is poured into the mouth where it mixes with the food. It is secreted in well-developed racemose glands, situated a short distance from the cavity of the mouth, into which the secretion passes by ducts leading away from each gland. There are three pairs of salivary glands. (1) The parotid glands, so called because they lie in front of each ear. Their ducts communicate with the buccal cavity just opposite the upper molar teeth on each side. These are the glands which in man become characteristically swollen in the disease known as 'mumps,' though the other salivary glands are also generally affected in this complaint. (2) The sub-

maxillary glands, which lie in the lower jaw on each side. Their ducts open at the side of the root of the tongue. (3) The sublingual glands, placed underneath the tongue in the floor of the mouth, with several ducts opening close together.

The salivary glands are developed in the embryo in the form of buds which spring from the epithelium lining the inside of the mouth. These buds are at first solid but gradually become hollowed out and undergo a process of ramification so as to form lobules which when fully developed are bound together with connective tissue. In their mode of origin and also structurally they may be regarded as typical of secreting glands generally.

Histologically there are two kinds of salivary glands, mucous glands and serous glands. The parotid glands are generally

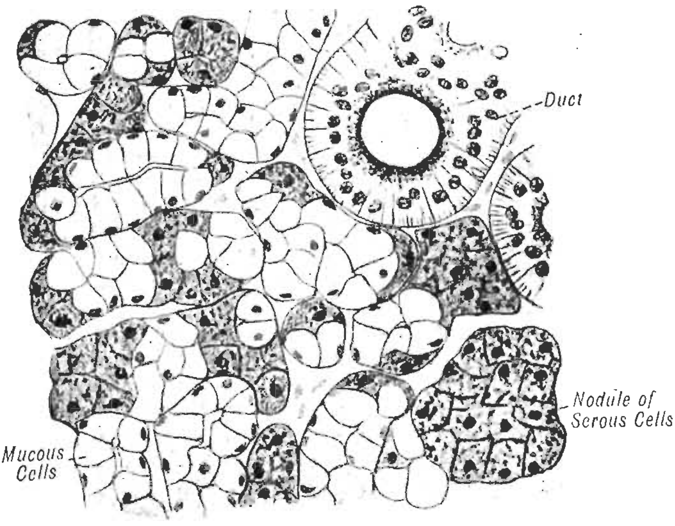


Fig. 20. Submaxillary salivary gland of dog.

composed of purely serous cells, whereas the submaxillary and sublingual glands are mixed glands, containing both mucous and serous constituents.

Each lobule of a salivary gland is composed of saccular or tubular alveoli or acini from each of which a duct passes, uniting with similar ducts from other alveoli to form the main duct of the gland. The alveoli are enclosed by a basement membrane within which are the glandular epithelial cells. In the case of

mucous alveoli these cells contain granules the number and position of which vary according to the condition of the gland, whether it is active or resting. The granules contain a substance called mucigen which is the precursor of the mucus to be discharged. In the resting state they are scattered over the greater part of the cell, the nucleus of which may be seen near one edge. During activity the granules are passed into the lumen part of the cell leaving the protoplasm of the cell relatively clear. In the cells of serous glands during rest the granular material is so abundant that the nuclei are occluded, only becoming visible when the gland passes into the active state. The nuclei are placed centrally. In the exhausted state the cells of serous glands retain only very few granules which are left on the inner edge near the lumen, which has grown larger, while the cells have become correspondingly smaller. The granules of serous glands like those of mucous glands represent the precursors of the secretion which is subsequently discharged. This account of the salivary glands is based on the observations of Langley upon the living glands and not merely upon glands which were preserved.

The salivary glands are as a rule well developed in herbivorous animals, but the submaxillary and sublingual glands are small and inactive in the horse. The parotid is four times the weight of the submaxillary and sublingual in the *horse*. The parotid in the horse is about half as heavy again as in the ox. (Ox 283 gs. Horse 400 gs.) The parotids (horse) secrete seven-tenths of the total salivary secretion. The parotid in all animals secretes more than the submaxillary or sublingual but it is not necessarily the largest in size. The amount of secretion discharged by the salivary glands depends upon the degree of dryness in the food, hay absorbing far more saliva than oats, and oats absorbing more than green fodder. Colin has estimated that a horse on an average will secrete 84 lbs. of saliva in a day, and an ox 112 lbs.

Mixed saliva is a viscid, turbid, colourless fluid with a slightly alkaline reaction. The viscidity is due to the presence of mucin, and the cloudiness to epithelial cells derived from the lining of the mouth, and to the salivary corpuscles. These are small granular cells, and may be altered leucocytes or lymphocytes derived from the tonsils. Saliva contains only about one per cent. of solid constituents altogether, and these include mucin (already mentioned) and other proteins in small quantities, a

ferment called ptyalin (not always present), and some inorganic matter. The salts found in saliva are chiefly carbonate of lime, alkaline chlorides, and phosphates of lime and magnesia. Calcium salts in the saliva are responsible for deposition of 'tartar' on the teeth. In human saliva potassium sulphocyanide is also present. The gases of saliva are carbon dioxide, which is very abundant, and traces of oxygen and nitrogen. The ferment ptyalin although present in human saliva and in the saliva of the pig is absent from that of the dog, and its occurrence in the horse and other herbivora is problematical. The function of ptyalin is to act on starch and convert it into maltose which is a sugar. Such starch-converting ferments are called diastatic or amylolytic. Their action is permanently destroyed by a high temperature and inhibited by a low one; it is also partly inhibited by weak acids or alkalis and destroyed by a strong acid. The chemistry of starch conversion by ptyalin is dealt with in the volume on nutrition.

As already mentioned the horse and ox and other herbivora masticate on one side only at a time, and it is interesting to note that the parotid glands in these animals to a large extent secrete unilaterally, that is to say, that the gland on the side where mastication is taking place secretes two or three times as much saliva as the gland on the opposite side; on the other hand the submaxillary and sublingual glands secrete equally on each side.

In addition to any ferment action which the saliva may possess, this secretion is of undoubted use in mastication and in deglutition. In the ox and sheep it is of use also in rumination.

The secretion of saliva is under the control of the nervous system, the process being brought about by a reflex mechanism. The afferent nerves are connected with the mucous membrane of the mouth, and the efferent nerves pass to the different salivary glands. Each gland has a double nerve supply, one from a branch given off the seventh cranial nerve and called the chorda tympani (in the case of the submaxillary and sublingual) or from the auriculo-temporal (in the case of the parotid), and the other from the sympathetic or thoracic autonomic system. There are two sets of nerves in the chorda tympani and in the auriculo-temporal, vaso-dilator and secretory. Stimulation of the chorda promotes dilatation of the blood vessels supplying the gland as well as secretion of saliva, but that the two processes are separate

(depending upon two sets of nerve fibres) is proved by injecting atropin, when stimulation of the nerve still produces all the vascular changes, but no saliva is secreted, the atropin having paralysed the secreting fibres without affecting the vaso-dilator fibres. The existence of a secretory process occurring independently of the vaso-dilator mechanism is further proved by the fact that the pressure of the saliva in the duct at the time of secretion may be greater than the blood pressure in the carotid artery, and consequently considerably greater than that in the capillaries of the gland. Moreover secretion may take place in the absence of blood, since after cutting off the head of a rabbit and immediately stimulating the chorda, salivary secretion can be induced. In the sympathetic two sets of fibres can also be demonstrated experimentally, these being secretory and vaso-constrictor, but the secretory fibres are comparatively few.

Further evidence of the existence of a definite secretory mechanism is afforded by the presence of mucigen granules, and the changes which take place during activity as described above, as well as by the fact that mucin and ptyalin do not exist as such in the blood, and therefore must be manufactured by the glands.

THE STOMACH.

The alimentary canal throughout its entire length is surrounded by several layers of tissue which have an essential similarity throughout its entire length. In those parts which lie freely in the body cavity there is an external serous or peritoneal coat consisting of fibrous tissue, and continuous with the mesentery or fibrous sheet which slings the gut in position and connects it with the inside of the body wall. Within the peritoneal coat are unstriated muscles arranged longitudinally and circularly, and within the muscular coat is connective tissue lined internally by a further thin muscular layer. The cavity of the alimentary canal is lined by an epithelium which varies in character in its different parts. In the mouth, pharynx and oesophagus, and in some cases the first part of the stomach, it is stratified and in function mainly protective, but in the secretory part of the stomach and in part of the intestine, the epithelium is columnar and depressed into tubular glands.

The stomach may be described as the dilated portion of the

alimentary canal at the posterior end of the oesophagus. It acts partly as a storehouse for food and so in man and many animals obviates the necessity for nutriment being eaten at short intervals, but it is also an important digestive organ in which the food is acted upon by the gastric juice secreted by the glands in its epithelial lining. The stomach is smallest and of least functional importance in carnivorous animals such as the dog which feeds on flesh to be converted into other flesh. In the dog the stomach may be removed and the organ completely dispensed with, without appearing to impair the digestive processes or the

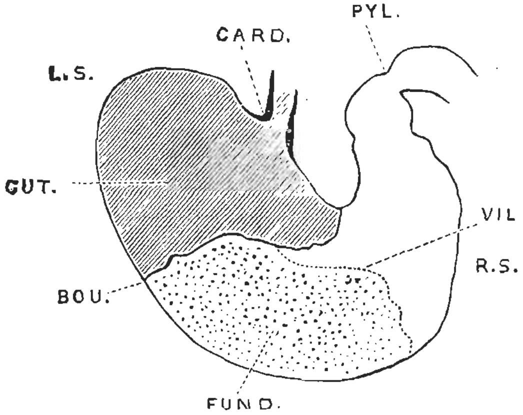


Fig. 21. Longitudinal section of stomach of horse (from Smith, Messrs Baillière, Tindall and Cox). *Card.* oesophagus, *Pyl.* pylorus, *L.S.* left sac., *R.S.* right sac. (or pyloric portion), *Cut.* cardiac portion, *Vil.* villous coat, *Bou.* boundary between cardiac and villous portions, *Fund.* fundus or villous portion.

health of the animal. In herbivorous animals in which the processes of digestion are necessarily more complicated since vegetable tissue has to be converted into animal tissue, we frequently find a very complex stomach, but this is not necessarily the case, for in the horse the stomach is small and simple, its place being taken functionally to a great extent by the extremely bulky large intestines which are reserved for the performance of digestive processes that in the ox and sheep take place in the rumen or first stomach. Thus maceration of vegetable fibre and decomposition of cellulose is carried out in the horse to a large extent in the colon and in the ox in the rumen.

It is noteworthy that the stomach of the pig is intermediate in character between that of the carnivorous dog and the herbivorous sheep, for the pig is not purely herbivorous, but, like man, can subsist on a very varied diet.

In the horse nearly one-half (the cardiac portion) of the internal lining of the stomach (that is, the mucous membrane) is merely of the nature of a continuation of the lining of the

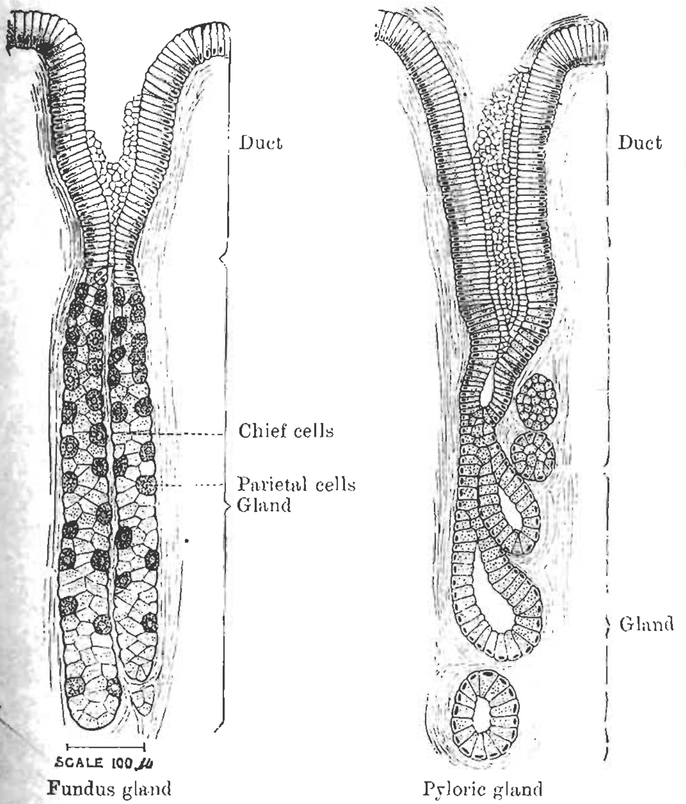


Fig. 22. Gastric glands (after Heidenhain from Smith, Messrs Baillière, Tindall and Cox). [The parietal cells are the acid-secreting ones.

oesophagus. This part which is sometimes called the proventriculus comes to an abrupt end and is succeeded by the secretory part or fundus. Here the tubular glands which secrete the gastric juice are separated by finger-shaped villous processes protruding into the cavity. The villous part is followed by a smooth pyloric portion which opens into the duodenum or first

part of the small intestine. As already mentioned the horse's stomach is relatively small, its average capacity being from 35 to 40 pints. It lies some distance from the body wall, being supported by the colon which is a part of the large intestine. Its cardiac and pyloric openings are situated close together, and the former is tightly contracted so as to make vomiting an act of great difficulty.

Pure gastric juice has not been obtained from the horse's stomach since owing to the distance between this organ and the body wall it has been found impracticable to establish an artificial connection between the secretory stomach and the outside of the body as Pawlow and others have done in the case of the dog.

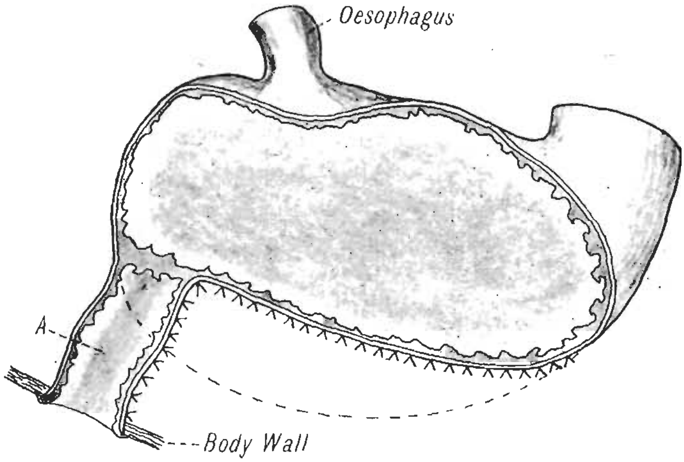


Fig. 23. Pawlow's fistula. The ∧ markings indicate the line of sutures. A = closed fundic sac. The broken line indicates the original outline of the stomach prior to operation.

Such a connection is called a gastric fistula, and the method of establishing it has been to make a cul-de-sac of the cardiac end of the stomach by reflecting the mucous membrane so as to form a diaphragm between the two cavities (that is the cavity of the cul-de-sac and the main cavity of the stomach), and to connect the cul-de-sac with the abdominal wall so that it communicates freely with the outside of the body in the manner shown in the diagram. The vascular and nerve supply to the cul-de-sac portion are allowed to remain intact. Pawlow also made an oesophageal fistula in the dog, so that the food which was

swallowed instead of entering the stomach forthwith passed out of the body.

A dog so operated upon will eat with avidity and may continue eating for hours, during which time gastric juice, free from admixture with other substances, passes out through the gastric fistula. The juice thus obtained is found to be a clear fluid with an acid reaction; it contains about one per cent. of solids and ninety-nine per cent. water. The solids consist of mucin, proteins, and inorganic salts. It also contains two ferments, pepsin which acts upon proteins and converts them into simpler substances, called proteoses and peptones, in the manner described in the second volume, and rennin, which changes caseinogen (the phosphoprotein of milk) into casein. There is however some reason to doubt whether rennin is in reality an independent ferment, since evidence has been brought forward suggesting that possibly the conversion of caseinogen into casein may after all be due to pepsin. This ferment can only act in an acid medium. In the dog and in man the acid present is hydrochloric. The lactic and other acids which are found in the gastric juice of herbivorous animals are probably produced by the bacterial decomposition of the food they swallow. As in the case of other ferments the activity of pepsin and rennin is permanently destroyed by boiling. The experiments by Pawlow described above indicate that the normal stimulus for gastric secretion is the presence of food in the mouth and that the process is of the nature of a nervous reflex. The truth of this presumption is established by the fact that secretion may not occur after the severance of the two vagus nerves which supply the stomach, and the further fact that electrical stimulation of these nerves is followed by secretion. It is clear therefore that the efferent nerves concerned in the reflex are the two vagi, while the afferent nerves are the sensory nerves of the mouth, possibly assisted by the nerves of sight and smell.

Edkins however has carried out experiments showing that there is also a subsidiary mechanism for gastric secretion, for in a dog in which the vagi have been severed and two gastric fistulae have been established with two artificially separated portions of the stomach, the introduction of food into one portion through the fistula connecting that portion with the exterior, may be followed by the outpouring of gastric juice through the other fistula. Moreover injection of *pyloric mucous membrane into the circulation*

of a dog so operated upon may be followed by gastric secretion. These experiments show that gastric secretion may result from the exciting action of an internal secretion normally produced in the mucous membrane of the pyloric portion of the stomach and passed into the blood in which it is carried to all parts of the body including the whole secretory area of the stomach where it evokes the activity of the gastric glands. The chemical excitant having the specific action described has been designated gastrin or gastric secretin, and it belongs to a class of internal secretions which Starling has called by the name of hormones. Such bodies are internal secretions having a specific stimulating action upon organs or tissues other than those which manufacture them.

There can be no doubt that the general principles underlying the mechanisms of digestion just described apply as much to the horse and other animals as to the dog. A further knowledge of the digestive processes in the horse has been obtained by means of feeding experiments.

It has been noted that under normal conditions in the horse the stomach is hardly ever empty. Even many hours after feeding, some food is still present, and it is not until a horse has been starved for twenty-four hours that its stomach is found to be really devoid of food. At the time of feeding, however, food usually passes out of the stomach into the small intestine with considerable rapidity, and when the stomach has become two-thirds full the rate of ingress of food and the rate of egress are equal. But as soon as the feed is finished the passage of the food into the intestine at once slows down.

The condition of the digesting stomach varies somewhat according to the nature and quantity of the food, and the order in which it is supplied. Hay after mixing with about four times its weight of saliva and after mastication in the mouth passes into the stomach, and if it be empty, the hay comes to lie in the pyloric region. As the stomach gradually fills it gets acted upon by the gastric juice, and some of it, in a partially digested state, commences to pass out into the intestine. At the end of the feed the material left in the stomach is found to be comminuted and to resemble green and yellow faeces, the colour being due to the acid of the gastric juice. The entire stomach is at this time generally acid throughout, and if any alkalinity can be detected it is caused by the swallowed saliva.

The duration of digestion of hay by the stomach has been worked out experimentally by Colin and by Smith. Colin found that the rate of digestion during the first two hours is rapid, but that it afterwards decreases so that at the end of eight hours some hay is still retained in the stomach. Smith starved a horse for twenty-four hours and then gave it 6 lbs. of dried grass; the horse was destroyed nine hours afterwards when the stomach contained 2½ lbs. showing that 3½ lbs. had been digested. Other experiments illustrated the same point, namely the increasingly slow rate of digestion the longer the time that had elapsed after a meal.

In digesting oats the same fact was observed. Smith found that in a horse which had received 2 lbs. and was killed twenty hours later the stomach was not empty.

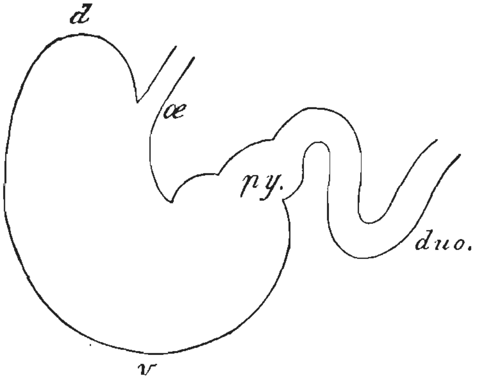


Fig. 24. Section through stomach of horse showing syphon-trap of duodenum (*duo*). *œ* oesophagus, *py.* pylorus, *d* left sac, and *v* fundus. (From Smith, Messrs Baillière, Tindall and Cox.)

If a horse be fed with different foods in succession these arrange themselves in the stomach in the order in which they enter, and pass out in the same order without mixing unless the horse is watered after its meal. The effect of watering is to disturb the arrangement of the food and to wash a large part of it, in a very undigested state, into the small and large intestine where it may produce irritation and colic. Hence, the importance of watering a horse before feeding and not afterwards.

The acids which are present in the digesting stomach depend partly upon the nature of the food. It has been said that hay induces an outpouring of lactic acid and oats of hydro-

chloric, but as already mentioned, it is a matter of great doubt as to whether lactic acid is ever actually produced by the stomach itself, the suggestion being that its presence is due to the fermenting food. Hydrochloric acid is unquestionably produced by the gastric glands; nevertheless lactic acid appears to predominate in the horse's stomach during digestion. The secretory part of the stomach produces also a quantity of mucin which frequently forms a gelatinous coat over the surface.

The pyloric aperture unlike the opening of the oesophagus is usually wide, and beyond this the small intestine is dilated. The passage of food out of the stomach is regulated by a U-shaped curve (sometimes called the 'syphon-trap' of the duodenum). When the large bowels become distended they press against this portion of the duodenum and close the pyloric outlet from the stomach, and if fermentation is taking place in the stomach, its contents may be unable to escape since the oesophageal opening is also contracted as already described. In such cases rupture of the stomach may supervene.

The stomach of the pig as already mentioned represents a transition stage between the simple stomach of the dog and the complex stomach of ruminants. There is an oesophageal patch without glands, which correponds to the proventriculus of the horse, and according to some authorities the rest of the stomach is divisible into three or four zones in which the number of glands and the secretory activity are somewhat different. Ellenberger and Hofmeister have found that the swallowed saliva has a strong amylolytic action on the carbohydrates in the pig's stomach and that conversion of starch into dextrin and sugar takes place to a marked extent, the sugar so formed becoming further converted into lactic acid. The cardiac end of the stomach is utilised for digesting starch while the pyloric half digests albumen, but the latter process begins at a later stage than the starch digestion and continues after it is over.

Rumination. In the ox and sheep and all ruminating animals the food after being swallowed for the first time does not ordinarily reach the true or digestive stomach until it has been first regurgitated to the mouth where it undergoes a second and more complete mastication. This process is called rumination or the chewing of the cud. It involves a complicated system of oesophageal enlargements which will now be described.

The food after being submitted to a slight chewing passes down the oesophagus and into a receptacle of great size called the rumen or paunch. Here it undergoes a churning movement and is acted on by the saliva which is swallowed with it. In the rumen cellulose is said to be digested through fermentative processes to as much as sixty or seventy per cent. This is due to the action of bacteria present in the food, for the rumen possesses no glands. Thus it corresponds functionally with the large intestine in the horse as will be made clearer later. The reticulum, which, from the ridges arranged in a honeycomb pattern on the inside of its walls, is often called the honeycomb bag, is an extension of the rumen. It acts as a reservoir of liquid which

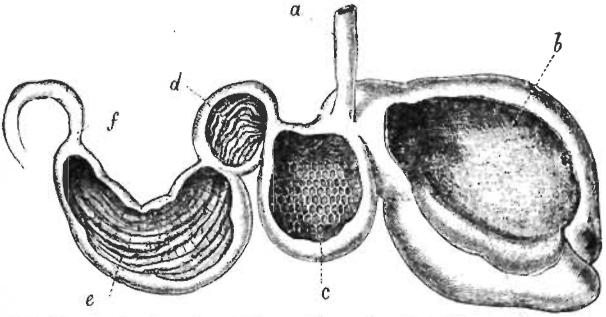


Fig. 25. Stomach of ruminant (from Flower and Lydekker). *a* oesophagus, *b* rumen, *c* reticulum, *d* omasum, *e* abomasum, *f* duodenum.

moistens the food before it is passed back into the mouth. The reticulum is not essential for rumination since Flourens showed that its excision did not inhibit the process.

The oesophagus is continued along the side of the rumen and reticulum in the form of a groove with lips or pillars which when relaxed admit of its communicating with the rumen and reticulum. During the churning movement which takes place in the rumen the food becomes pressed against the lips of the groove. This sets up a spasmodic contraction of the muscles of the abdomen and diaphragm, as a result of which some of the food enters the lower part of the oesophagus and is carried upwards by peristaltic waves passing upwards along the muscles of that organ. In this way the food is regurgitated to the mouth. The liquid part of it is at once reswallowed, but the more solid part is masticated afresh for a considerable period, during which time it is acted on by the parotid saliva. It is then swallowed a second time

and after being carried down the oesophagus passes along the oesophageal groove and enters the omasum or third stomach, frequently called the manyplies owing to the wall being thrown into folds which resemble the leaves of a book. Some of the food, however, may return once more to the rumen. Whether the food is to enter the rumen or the omasum appears to be determined by its condition. It is only allowed to pass into the third stomach if it is in a sufficiently divided condition. Its entry is effected by the contraction of the lips of the groove. In this way the rumen and reticulum are shut off and the oesophagus communicates directly with the omasum.

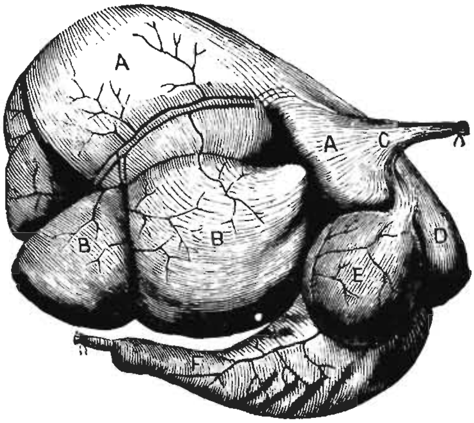


Fig. 26. Stomach of ox (from Smith, Messrs Baillière, Tindall and Cox). *A* and *B* rumen, *C* oesophagus, *D* reticulum, *E* omasum, *F* abomasum.

This compartment is not concerned in the process of rumination. Its chief characteristic is its strong muscular leaves lined with coarse stratified epithelium. These act as a triturator and strainer, and prevent food substances passing into the abomasum or fourth stomach until they are in a sufficiently fine state of division.

The abomasum is the true digestive stomach corresponding with the fundus portion of the horse's or pig's stomach. In it are the glands which secrete the gastric juice containing pepsin, and the other substances which are present in the gastric juice of the horse. It is interesting to note that in the sucking ruminant (e.g. the calf and lamb) the abomasum is the only compartment which is functional, the first three stomachs being com-

paratively undeveloped. This is because the young animal does not ruminate, and has no need for bulky receptacles for cellulose digestion.

Rumination is a reflex act, the centre for which is in the medulla. The efferent nerves are the sensory nerves of the rumen. The process depends on the united action of the diaphragm, stomach and abdominal muscles. The amount of food contained in each ascending bolus in the ox is about 3½ to 4 ounces. The formation of the bolus and its ascent to the mouth occupy 3 seconds; the actual process of chewing the ascended cud generally lasts about 50 seconds; and the descent of the bolus 1½ seconds. Colin has estimated that out of 24 hours, about 7 are occupied by rumination.

During rumination the animal lies slightly on one side, and rests partly on its chest and partly on its abdomen, its fore limbs being bent under its chest, and its hind limbs brought forward so as to lie partly under its body. This is the familiar attitude of cows chewing the cud. They are usually very timid, and any slight disturbance causes them to get up and rumination is brought temporarily to an end. So also fatigue, or the occurrence of slight maladies or excitement due to oestrus, may interfere with rumination, and the longer it is delayed the more difficult it is to resume since the food becomes dry and closely packed, so that it is liable to set up local irritation.

The Small Intestine and the Glands communicating with it.

The intestinal canal or alimentary canal beyond the stomach is divided into two main parts, the small intestine, and the large intestine. The small intestine is comprised of the U-shaped *duodenum* which immediately succeeds the pyloric end of the stomach, and the *ileum* which is considerably longer and is usually much coiled. The middle portion of the small intestine is sometimes called the *jejunum*.

The small intestine is composed of the same four coats as the stomach, serous or peritoneal, muscular, submucous, and mucous, the latter being lined internally by a columnar epithelium. There are numerous vascular villi confined to the mucous membrane. These are provided with vessels containing lymph, and

each villus is covered by a columnar epithelium resting on a fine basement membrane. This epithelium is continuous with that lining the rest of the mucous membrane. Beneath the basement membrane is a rich supply of blood vessels.

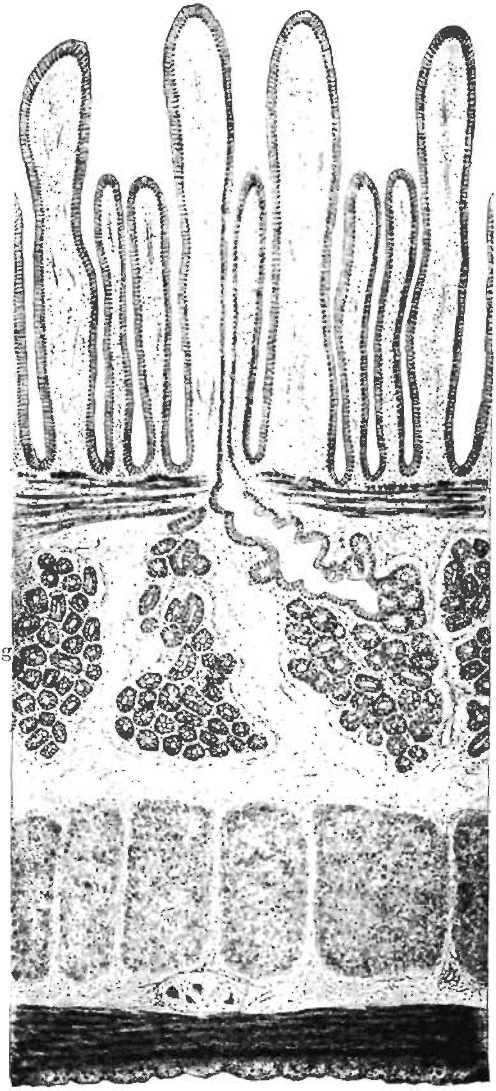


Fig. 27. Section through wall of duodenum (from Schafer.)

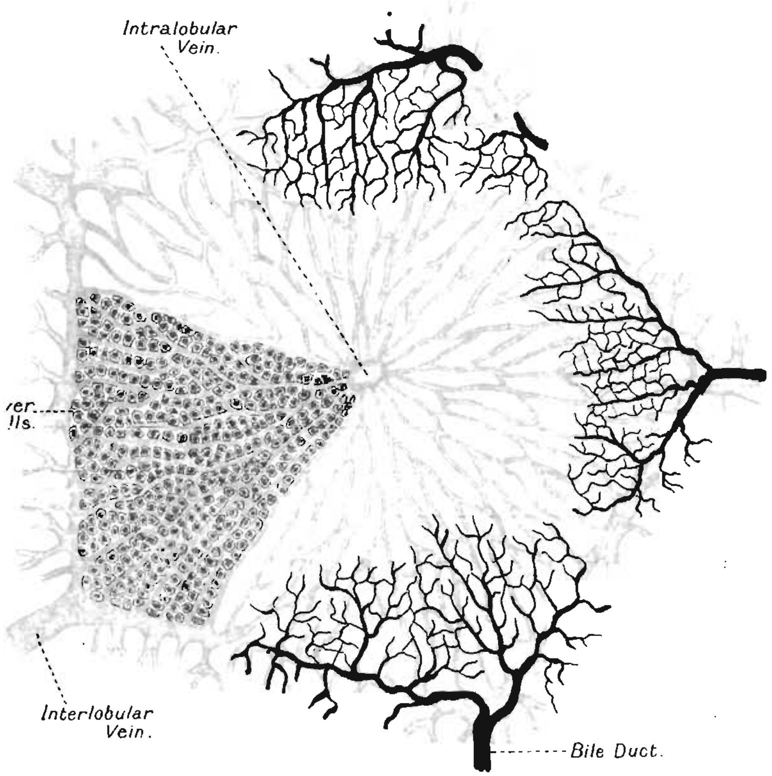


Diagram of Liver Lobule showing distribution of bile ducts, blood vessels and liver cells.

lith. Cambridge University Press

There are two kinds of glands in the small intestine, the so-called crypts of Lieberkühn and Brunner's glands, but the latter are restricted to the duodenum, not being found in the ileum. The crypts are tubular depressions in the mucous membrane, and occur also in the large intestine, being very numerous throughout the greater part of the intestinal canal. Brunner's glands are situated in the submucous tissue of the duodenum and communicate with the lumen by ducts which traverse the mucous membrane. They are especially numerous in the horse. We also find numerous patches of lymphoid tissue in the mucous coat of the small intestine. These are similar to the tonsils which are two larger lymphoid masses at the entrance to the pharynx. Those occurring in the small intestine are known as Peyer's patches.

Lieberkühn's and Brunner's glands secrete the succus entericus or digestive juice of the small intestine. The ferments present in this juice and their action on the different classes of food are described in the second volume.

The Liver. Communicating with the duodenum by the bile duct is the liver which is the largest gland in the body. It is composed of round, oval or polyhedral lobules consisting of the liver cells among which ramify the branches of the bile duct and numerous blood vessels and lymph vessels. The lobules are separated by connective tissue, and in the pig this separation is complete, but in man and many animals is incomplete; the lobules however become more perfectly divided as a result of certain diseases such as alcoholism in which case the liver in man comes to resemble that of the pig. The blood supply of the liver is peculiar, for besides receiving arterial blood from the hepatic arteries it is provided with a large quantity of venous blood which is brought to it by the portal vein from the stomach, spleen and alimentary region. It is obvious, therefore, that a great variety of metabolic products must be brought to the liver, and correlated with this fact we find that the liver discharges a number of important functions connected with the general metabolism of the body. It stores up carbohydrate material in the form of glycogen, releasing it into the blood as sugar, the percentage of which is thereby kept constant; it makes urea and uric acid which are discharged as waste products by the kidneys; and it manufactures bile which is poured out into the small intestine and utilised there for digestive purposes.

The bile contains the waste products of the liver which result from its other activities. Nevertheless when associated with pancreatic juice it is of considerable importance in the process of fat digestion; moreover it promotes intestinal peristalsis, its absence leading to constipation. Bile is an alkaline fluid of a slimy consistence and with a bitter taste; in herbivorous animals it is yellow-green or dark green, in the pig reddish-brown, and in carnivorous animals golden red. The differences in colour depend on the bile pigments of which bili-rubin and bili-verdin are the chief. Its composition is approximately as follows:

Water, 85 parts,
Bile salts, 10 parts (glycocholate and taurocholate of soda),
Fats, lecithin and cholesterin, 1 part,
Mucus and pigments, 3 parts,
Inorganic salts, 1 part.

The secretion of bile occurs under a pressure lower than that of the blood, and in this respect is different from the salivary secretion. There is no evidence that nerve fibres are concerned with bile secretion which seems to be controlled by the composition of the blood carried to the liver and by the activity of the liver cells. There is some evidence that the secretion is stimulated by a substance called secretin which is liberated from the wall of the duodenum and is of the nature of a hormone or chemical excitant. This substance, however, acts chiefly upon the cells of the pancreas as will be described below.

The bile is either conveyed directly by the bile duct into the duodenum or by the cystic duct into the gall bladder, in which it is retained until required; it is then poured out into the duodenum by the bile duct. The latter opens a short distance from the pyloric end of the stomach. In some animals there is no gall bladder. This was pointed out long ago by Aristotle who records its absence in the horse, ass, deer and roe. It is also absent in the elephant, tapir and rhinoceros, and is imperfectly developed in the camel. In the ox, sheep, pig, and all carnivora it is present. In man it is present with a few individual exceptions, as noted by Aristotle, whose observations on this subject show a remarkable accuracy. It has been suggested that the gall bladder is absent in the horse because this animal in the natural state is constantly eating, and consequently the continual outpouring of bile into the intestine is beneficial,

whereas its presence in the sheep and ox has been attributed to the fact that these are ruminating animals in which the passage of food into the duodenum only occurs at stated intervals when the presence of bile is desirable, the fluid being stored in the gall bladder between whiles. This explanation, however, is scarcely adequate in view of the facts recorded above that the deer and roe which ruminate have no gall bladder, whereas the pig which does not ruminate possesses one.

Obstruction of the bile duct, due for example to a flux of mucus leading to its closure, or to disease, causes the bile to pass into the blood, and this produces the disease known as jaundice.

The Pancreas. The sweetbread or pancreas is a diffuse gland lying in the loop of the duodenum and communicating with it by a duct which usually opens into its ascending portion. In the horse and the sheep there is a common aperture for both bile duct and pancreatic duct but in the ox, pig and dog the

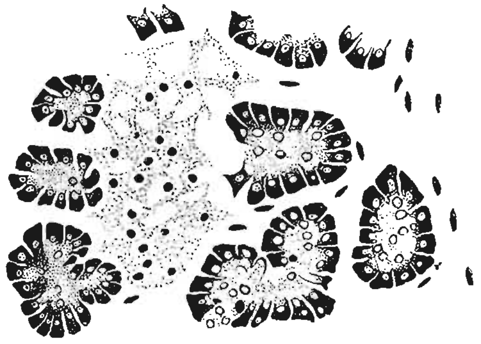


Fig. 29. Section of pancreas (after Harris from Halliburton), showing alveoli and islets of Langerhans.

ducts open separately. In structure the pancreas presents a general similarity to the salivary glands, but in addition to the secretory alveoli it contains certain cells which have a different staining reaction and do not communicate with the secretory ducts. These constitute the islets of Langerhans and are referred to again later in describing the pancreas as an organ of internal secretion. The secretory cells contain granules which are probably zymogenic. They disappear after prolonged activity of the gland.

Pancreatic juice, which is colourless and alkaline in reaction. in an animal with a pancreatic fistula makes its appearance between five and twenty minutes after a meal. Two or three hours later its quantity is considerably increased and after five hours it ceases to flow. The time of maximal flow, therefore, is when the contents of the stomach are being passed out into the duodenum. Bayliss and Starling have shown that the main factor in producing pancreatic secretion is chemical, but it is possible that nervous action may play a very small part in the initial stages of secretion. The pancreas is activated by a hormone, called secretin, which is liberated from the wall of the duodenum (where it is present as prosecretin), through the action of hydrochloric acid, the normal stimulus being derived from the passage of the gastric contents into the duodenum. Bayliss and Starling have shown that after the nerve supply of the pancreas has been cut off injection of acid extract of duodenal mucous membrane into the circulation results in an almost immediate flow of pancreatic juice. The acid converts the precursor prosecretin into the activating hormone secretin.

The Ferments of the Pancreas and Small Intestine. The ferments present in the pancreatic juice are of great importance. They are as follows: (1) trypsin, which is a proteolytic ferment like pepsin but has the power of breaking down the protein molecule still further, and can change proteins into amino-acids of which leucine, tyrosine, and tryptophane are examples; (2) amylopsin, which, like ptyalin, acts on starches and converts them into sugars, and (3) steapsin, which splits fats into fatty acids and glycerin. The fatty acids are then able to unite with the alkalis of the bile salts to form digestible soaps.

The succus entericus contains the following ferments: (1) maltase, which converts maltose into dextrin and dextrose; (2) invertase, which converts cane sugar into dextrose and levulose; (3) lactase, which converts lactose into dextrose and galactose, and (4) erepsin, which converts peptones into amino-acids. It also contains (5) enterokinase, which is a necessary factor for changing the trypsinogen present in the juice secreted by the pancreas into the active ferment trypsin. For trypsin does not exist as such in the juice produced by the pancreas, but is only present in pancreatic juice which has been brought under the influence of enterokinase.

Seeing that pepsin can convert proteins into peptones and erepsin can further change peptones into amino-acids it has been suggested by Reynolds Green that trypsin is in reality composed of a pepsin-like ferment together with an erepsin-like ferment.

Erepsin is also manufactured by the pancreas, and according to Vernon all (or nearly all) the tissues of the body have certain ereptic properties and may therefore be regarded as forming this ferment to a greater or less extent.

Absorption. It is seen that by the time that the different classes of foods have reached the hinder part of the small intestine, they have all been brought under the influence of digestive agencies, and so have to a large extent been reduced to a condition of solution in which they can be absorbed into the circulatory system. Absorption from the stomach is non-existent or extremely slight, though it is said to occur to a somewhat greater extent in the pig than in most other animals. As will be seen later the large intestines are the main absorbing area of the alimentary canal in many animals. Nevertheless, in all animals, absorption is carried on to a very large extent in the small intestine and the villi which are very numerous are evidently constructed to that end.

These villi contain lymph vessels (lymphatics and lacteals) which eventually communicate with the blood circulation. Fat in the form of small globules is carried by leucocytes directly into the lacteals. Moreover, the fatty acids dissolved in the bile together with the glycerine are absorbed by the living cells of the villi and recombined to form fat. The villi also contain blood vessels and a small portion of the fat is absorbed directly into the circulation and carried to the liver or is retained as fat in the gut wall. The sugars (dextrose, levulose and galactose) are also absorbed by the villi. Absorption in the small intestine does not affect the products of protein digestion to the same extent as the fats and carbohydrates, nevertheless amino-acids as well as some of the intermediate products of digestion (e.g. peptones) of this class of food stuffs are also absorbed by the villi. It was formerly thought that proteoses and peptones were recombined to form proteins during their passage through the epithelial walls of the intestine, since the blood even in the portal area does not normally contain any trace of peptone or proteose. Later evidence has shown that most, if not all, of the

protein is absorbed by the gut in the form of amino-acids; and as by improved technique it has been shown that amino-acids are normally present in the blood, there is little reason still to believe that these amino-acids are re-synthesised into protein within the walls of the intestine. Water and salts are absorbed and taken up by the blood vessels with great rapidity.

The inlet and outlet to the small intestine are regulated by sphincters. The total length of the small intestine in the horse is about 70 feet; that of the ox is 130 feet, but the diameter is very much smaller. The small intestine in the sheep is 80 feet and in the pig 60 feet. It has been found that in the horse water takes from five to fifteen minutes to traverse the length of the small intestine; semi-digested food takes a much longer time.

The Large Intestines.

The large intestines comprise the colon, the coecum, and the rectum. Each of these parts is composed of the same four coats as the small intestine. Lieberkühn's crypts are represented, but there are no Brunner's glands and no villi (excepting in the coecum in the horse and some other animals) neither are Peyer's patches to be found. In man and some animals an ileo-coecal valve at the entrance to the large intestine prevents a reflux into the small intestine. It is made up of two semilunar folds of the mucous membrane.

The coecum varies in importance according to the character of the food. In man it is a short wide pouch ending with the small appendix vermiformis which is largely composed of lymphoid tissue; it is this structure which is frequently removed surgically as a consequence of the inflammatory condition or infection known as appendicitis. In the carnivora the coecum is likewise vestigial or absent. In all herbivora on the other hand it is large and functional.

In the horse the capacity of the coecum is enormous, being about 8 gallons (while its length is 4 feet). It acts as a reservoir for intestinal digestion. Everything must traverse it in passing from the ileum to the colon. The two openings are placed near together, and the outlet is above the inlet, so that the substances it contains have to pass out against gravity in order to enter the colon. The contents of the coecum are always fluid and sometimes watery; their reaction is alkaline. Its main function is

probably to store water required for intestinal digestion and for the general wants of the body, but the digestion of cellulose is undoubtedly one of its functions. This substance undergoes churning, maceration and decomposition and is thereby reduced to a condition in which it can be absorbed. Ellenberger has shown that in the horse the entire 'feed' reaches the coecum at

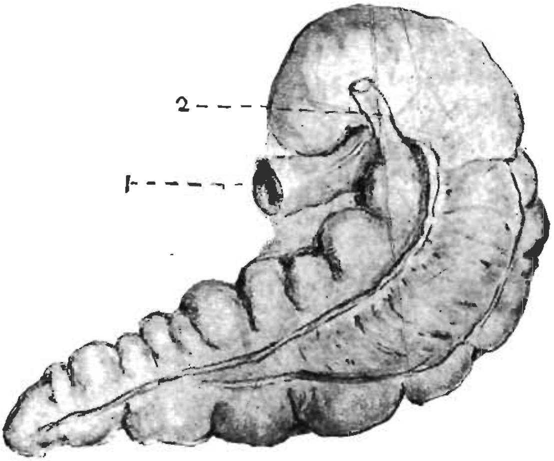


Fig. 30. Coecum of horse (from Smith, Messrs Baillière, Tindall and Cox). 1 Beginning of colon. 2 End of ileum.

some time between twelve and twenty-four hours after entering the stomach, that it may remain in the coecum for twenty-four hours, during which time twenty per cent. of the cellulose may disappear. There can be no doubt that absorption occurs in the coecum to some extent. Poisonous products are removed from it and carried by the blood to the liver.

In the ox and sheep, in which cellulose digestion is known to take place in the rumen, the coecum is much smaller than in the horse. In the pig it is still smaller relatively to the size of the animal.

The colon in the Carnivora is of small importance, acting chiefly as a reservoir for the excrement which becomes somewhat drier as it passes along it. In the herbivora, and particularly in the horse, it is the main absorbing part of the gut. Its glands liberate mucus, but do not produce ferments. It also has an excretory function for metallic salts leave the body by this channel.

Digestion continues in the colon and is therein terminated, but the process is carried on either by ferments passing into it along with the food from the anterior part of the gut or else by bacterial disintegration as happens in the horse. It has been shown that bacteria may hydrolyze cellulose, and that in the case of oats there is evidence that a digestive ferment is present in the food itself. In the horse particles of corn and other comparatively unaltered food substances are found in the first part of the colon, but as we pass on the food becomes more and more fluid, then firmer again, and in the last part the contents are like thick pea soup containing finely comminuted particles. In ruminants the function of the colon is only subordinate, since, as already mentioned, cellulose digestion is carried on at the anterior end of the gut. In the pig also the colon is of relatively small importance.

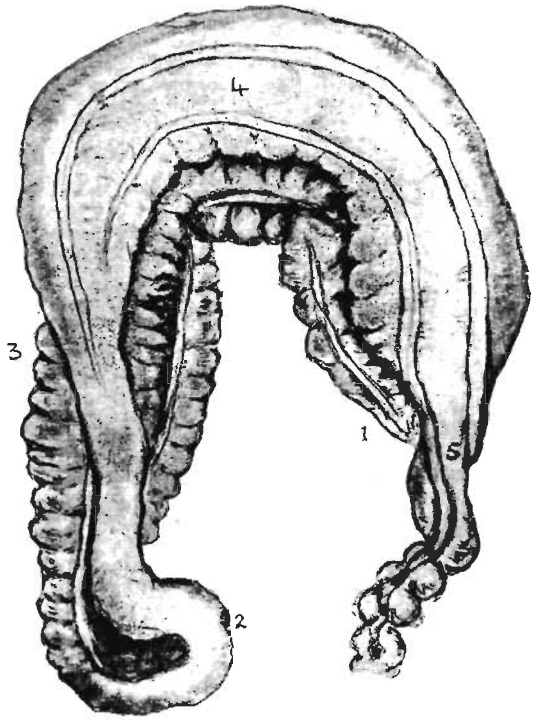


Fig. 31. Colon of horse (from Smith, Messrs Baillière, Tindall and Cox) 1 first colon, 2 pelvic flexure, 3 suddenly enlarges, 4 diaphragmatic flexure, 5 commencement of single or small colon.

It remains to describe the colon of the horse, in which animal this portion of the gut is better developed than in any other. It begins by being very narrow, but rapidly swells out to an enormous size. The first part is high up lying a little below the vertebral column and to the right side. It then passes downwards to the floor of the abdominal cavity where it is very large as just mentioned. It next ascends in the direction of the pelvis, and makes a curve of two right angles. The curved part being very small, it then passes forwards and on top of the part already described. Near the diaphragm it passes first downwards and then upwards and backwards again, meanwhile increasing in size to form the enormous double colon: the calibre of which is greater than that of any other part. Finally it suddenly contracts becoming the single colon. It is obvious that such a large and complicated structure must be of great importance functionally, and there is every evidence that this is actually the case. Its huge capacity, which is five or six times that of the stomach, admits of it retaining great quantities of food substances and fluids which are brought into contact with a large absorptive area of the lining of the gut wall.

The following are the dimensions of the colon in the domestic animals:

		ft	diam.
Horse	Great Colon	10 to 12	8 to 10 inches
	Small Colon	10 to 12	3 to 4 ,,
Ox		35	5 to 2 ,,
Sheep		15	2 to 1 ,,
Pig		11 to 14	

The Rectum. The faeces consisting of indigestible residue collect in the lower part of the colon and then pass into the rectum from which they are ejected through the anus. In all animals they vary to a greater or less extent according to the diet, and according to the amount of the excretory products of the digestive tract. If no food is given, they consist solely of the latter, and the same statement holds good if the food is completely digested as may happen with the dog when somewhat underfed on an exclusively meat diet.

In the horse the faeces are generally firm and brownish-red in colour. They contain cellulose, husks of grain, vegetable tubes, starch and fat globules, etc. together with bile pigments and other excretory products. In the ox the faeces are semi-solid.

and greenish-brown in colour. In the sheep they are small solid balls, black or dark green. In the pig the faeces are generally semi-solid and human-like with a variable colour and very disagreeable smell. In the dog they are very variable, being often gray owing to the presence of lime salts (due to eating bones) and dense in consistency.

As to the amounts of faecal matter passed, the ox averages a very large amount, as much as 75 lbs. a day, the horse passes 30 lbs. a day (the maximal amount being over 70 lbs. a day), the sheep about 4 lbs. and the pig approximately the same. The quantity passed relatively to the amount of food is less in the carnivora.

Defaecation is usually in animals a reflex act due to the presence of faeces in the rectum. It is brought about by the rectal muscles assisted by the muscles of the abdomen, though these are not essential since horses can defaecate while trotting. The centre for defaecation is in the lower part of the spinal cord. The sphincter of the anus is relaxed during the process. It contains striated muscles, showing that defaecation may be partly a voluntary process.

The volume of the stomach and that of the rest of the alimentary canal in the different animals, according to Colin, are as follows:

	Stomach	*Intestinal Canal*
Horse	31 pints	340 pints
Ox	440 ,,	183 ,,
Sheep	52 ,,	26 ,,
Pig	14 ,,	34 ,,
Dog	6½ ,,	14 ,,

These results are in general agreement with the statements of more recent authorities.

In addition to the movements of the alimentary canal already referred to (such as swallowing, defaecation, etc.) we find that in the presence of food peristaltic waves of contraction are continually passing down the intestine and urging forward the masses of food. Peristalsis of a weaker character in which the constriction of the alimentary tube is very incomplete, also takes place, and this serves to propel the outer layer of food and so brings a new supply into contact with the gut wall. The walls of the stomach (and in ruminants the proventriculus or rumen) undergo contractile movements which set up surface currents involving the

food in their immediate neighbourhood. In this way the rotatory motion of the contents of the rumen is produced.

These movements are under the control of a network of nerve fibres and ganglia, which though they are capable of going on in the absence of any connection with the spinal cord, are normally under the subordination of the central nervous system through autonomic nerves. The cranial autonomics through the vagus nerve supply the whole of the alimentary canal excepting the hind part of the colon and the rectum. Impulses transmitted along them excite muscular movement and increase peristalsis. In the hind part of the gut they are replaced by sacral autonomics. The whole of the gut is supplied by sympathetic or thoracic autonomic nerves which in a general way act antagonistically to those above mentioned. Impulses transmitted along them decrease muscular movement, and by constricting the blood vessels reduce the blood supply. The gut is also supplied with sensory nerves conveying the sensations of hunger, pain, etc.

The whole of the gut is well supplied by blood vessels bringing arterial blood from the aorta. The veins of the alimentary tract as already described unite to form the portal vein, so that the blood drained from the gut cannot reach the heart and join the general circulation without first traversing the liver.

The lymphatic vessels discharge their contents either into the large thoracic duct which opens into the left anterior vena cava between the subclavian and jugular veins or else into the corresponding smaller right lymphatic trunk which communicates with the right vena cava. Through these vessels the lymph is passed into the blood vascular system.

CHAPTER IV

THE BLOOD AND THE ORGANS OF CIRCULATION

Every part of the body with few exceptions is to a greater or less extent vascular, that is to say, it is permeated by vessels through which the blood is continually circulating. The blood is the medium by which nutritive substances, water, salts, and oxygen are conveyed to all parts of the body, and it is through this same medium that the waste products are carried away to be eventually disposed of by the organs of excretion or respiration. Moreover, the substances manufactured by the internally secreting glands together with other chemical bodies, are likewise transported by the blood. Lastly, by circulating rapidly through all the tissues, the blood helps to keep the temperature of the animal approximately the same throughout.

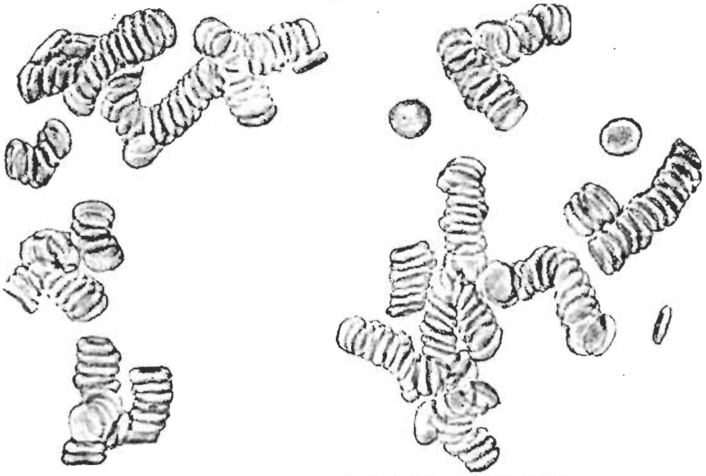


Fig. 32. Human red blood corpuscles (from Schafer).

As seen in quantity blood is a red opaque fluid, but when examined in thin layers under the microscope it is found to consist of corpuscles of two kinds floating in a yellowish coloured liquid, the blood plasma. The erythrocytes or red corpuscles

(appearing yellow when looked at singly) are by far the most numerous, there being about 500 of these to one leucocyte or white corpuscle in normal human blood The erythrocytes in nearly all mammals are minute, circular, biconcave discs. They have no nuclei. They consist of protein material containing a red-coloured substance called haemoglobin, which itself can be resolved into a protein and an iron-containing substance termed haematin. The leucocytes are generally slightly larger, but vary

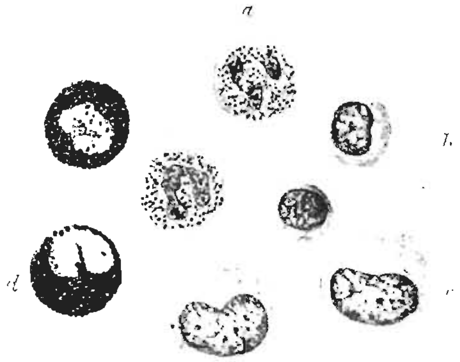


Fig. 33. White corpuscles or leucocytes from blood (from Schafer). *a*. polymorph, *b*. lymphocyte, *c*. macrocyte, *d*. eosinophil.

in size according to the variety to which they belong; they are round or amoeboid in shape, and may have one or more nuclei, and they possess the power of independent movement. Some of them are phagocytic and can ingest bacteria or other foreign bodies after the manner of an amoeba. They tend to congregate in any area of inflammation or disturbance, and one of their main functions is undoubtedly to protect the organism against disease or the results of injury. They have different staining reactions according to kind, some having acid and some basic affinities.

The red corpuscles are produced in bone marrow, which is richly supplied with vessels. Certain kinds of white corpuscles also have their origin in bone marrow, but others are formed from the lymphocytes of the lymphatic glands.

Blood which has been recently shed also contains platelets, which are circular bodies smaller than corpuscles. They have been supposed to represent nuclei extracted from erythrocytes in the process of their development, but it is uncertain whether they are really present in normal unaltered blood.

The blood plasma contains about ninety-two per cent. water, and the remaining eight per cent. consists of proteins, fats, carbohydrates, salts and gases, and all the various products of metabolism which need to be transported to or from the different parts of the body. The proteins consist largely of albumen and globulin together with fibrinogen which as mentioned below plays an important part in the process of clotting. The reaction of blood plasma is alkaline.

If blood is withdrawn from the body and allowed to stand in a vessel for a short time (three or four minutes for a man or a little longer for a horse) it becomes thick and eventually coagulates or clots. After a space of a few hours the clot shrinks like curd of milk, and finally we get a tangled mass containing the corpuscles enmeshed in it, floating in a colourless fluid which is called serum. The network of the tangled mass or clot consists of fibrin, a protein substance white and stringy in appearance, and produced by the alteration of fibrinogen under the influence of another substance of unknown composition called thrombin. Thus, pure fibrinogen obtained by repeated precipitation is without the property of spontaneous coagulation, but if a little serum be added coagulation proceeds to take place, since the serum contains thrombin. Moreover, serum from the pericardial or other cavities will sometimes not clot spontaneously, but on the addition of other serum coagulation sets in. This again is explained on the assumption that the pericardial serum did not contain thrombin, but that this substance was introduced in the addition of other serum. It seems certain that thrombin is not a ferment, since its activity is not permanently destroyed by boiling.

Thrombin, like fibrin, is not present in the blood as such, but in the form of a precursor called prothrombin or thrombogen, from which it is converted through the agency of thrombokinase in the presence of lime salts. Normally however, if lime salts are not present (e.g. if they have been precipitated out from freshly shed blood, as by adding potassium oxalate) the blood will not clot. The thrombokinase which is formed in injured animal tissues and escapes into the blood, brings about the union of the lime salts with prothrombin, the resulting product being thrombin. This explains why it is that blood clots readily when in contact with broken or torn vessels, but does not easily do so in uninjured tissues, since thrombokinase does not occur (at any

rate in any great quantity) in normal healthy tissues. To recapitulate, when a vessel is ruptured so that blood escapes from it, the injured vessels will liberate thrombokinase. This thrombokinase enters into the blood, and there it finds all the necessary factors for the production of thrombin: it finds prothrombin and calcium salts. Thrombin is therefore formed, and this causes the fibrinogen to coagulate very quickly. This clotting helps to stop bleeding, and if the injury is slight allows the wound to heal without further loss of blood.

The Heart. The blood is kept in constant circulation through the vessels by the heart which acts as a double pump, the right and left portions of which have no direct communication with each other. The heart is situated between the lungs in a chamber called the pericardium. This is of the nature of a double bag, one covering forming a thin layer closely adherent to the heart itself, while the other or outer one envelops the heart more loosely. Between these two coverings is the pericardial fluid which is a form of lymph. The right and left portions of the heart referred to above each consist of an auricle and a ventricle. These are divided from one another by a movable transverse partition and communicate with one another by valves which admit of the blood flowing in one direction only, namely from the auricle to the ventricle. The apex of the heart is at the end of the ventricular portion which has a much thicker wall than either of the auricles. The valves just mentioned are of the same type on each side of the heart, but whereas the one on the right side has three flaps (the tricuspid valve) that on the left side has only two flaps (the mitral valve). Each flap is fastened at the base to the auriculo-ventricular junction, while its free end points towards the ventricle. The free edges of the flaps are connected by tendons, the chordae tendineae, to muscular processes (the musculi papillares) on the inner walls of the ventricle, and these prevent the flaps from being carried backwards into the auricular cavity when the ventricle becomes full of blood. Consequently, whereas increased pressure in the auricle forces the blood to flow into the ventricle by the flaps opening, the reverse process cannot take place excepting in certain kinds of heart disease when the valves are damaged or do not properly close. Coming away from each ventricle there is an artery (pulmonary artery on right side and aorta on left) which is provided with valves of another type.

These are of the nature of pouches, three in number, and having their free edges inside pointing away from the ventricle. These free edges separate under pressure and admit of the passage of the blood from the ventricle, but close together when the pressure is in the opposite direction, the pouches being then distended. The name semilunar valves has been given to them owing to their shape.

The blood is kept in motion mainly by the rhythmical contraction and dilatation of the heart, the alternating periods or conditions being called systole and diastole. Systole begins with the great venous trunks (the two superior venae cavae and the inferior vena cava) and then passes to the right auricle which undergoes a sharp contraction. The left auricle into which the pulmonary veins open contracts simultaneously with the right auricle. The wave of contraction then extends through the tissue dividing the auricular from the ventricular part of the heart to the ventricles which contract very powerfully, forcing the blood into the pulmonary arteries on the right side and the aorta on the left. The heart then expands previous to another contraction. As is well known the movements of the heart are entirely involuntary. Nevertheless the organ is well provided with nerves, there being two chief sources of supply, those from the vagus or tenth cranial nerve, and those arising from the sympathetics. The former are inhibitory, checking or controlling the heart's activity, while the sympathetic nerves are accelerator in function. There is a cardio-inhibitory centre in the hind brain, and when this is stimulated to excess (as in fainting or sudden emotion) it temporarily (or sometimes permanently) stops the heart's action. On the other hand stimulation of the sympathetic supply quickens the heart beats and may induce palpitation. Apart however from the nerve supply it is the essential property of heart muscle to undergo rhythmical contractions as may be seen when the organ is withdrawn from the body and placed in a glass vessel, while at the same time it is perfused with a fluid resembling blood serum (e.g. Ringer's solution). Under these conditions the heart will continue to beat in the same manner as it does normally when fulfilling its usual bodily functions. Moreover, in the case of some animals (e.g. tortoises) even small pieces of heart muscle will continue to undergo contractions after being removed from the rest of the heart.

In the horse, and various other Ungulata in addition to the chordae tendineae, there are other bands of tissue traversing the ventricles. These are the moderator bands; they pass from wall to wall, and their function is to restrain the ventricles from

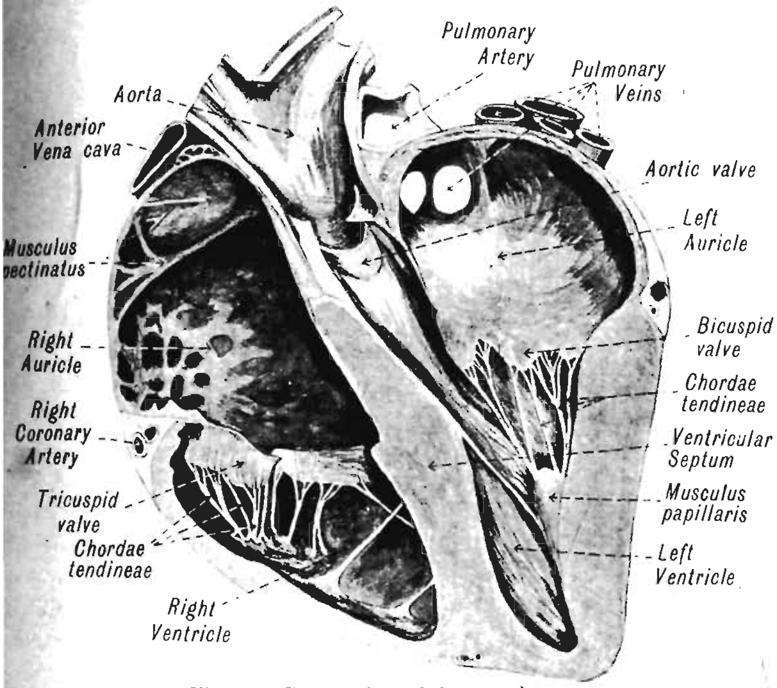


Fig. 34. Section through heart of horse.

undergoing undue distention. For this purpose they are especially well developed in antelopes and other animals which are fleet of foot, and in which cardiac strain might be supposed to be exceptionally great.

The complete course of the circulation in a mammal may now be described. The venous blood coming from all parts of the body enters the right auricle by the superior and inferior venae cavae. It passes through the tricuspid valve to the right ventricle; thence it proceeds by the pulmonary artery which gives off a branch to each lung; in so doing it is forced through the semilunar valves. In the lungs the blood undergoes the gaseous exchange which is an essential part of the respiratory process, yielding up the waste carbonic acid gas, and absorbing

oxygen. The purified or oxygenated blood then traverses the pulmonary veins which convey it to the left auricle; from this chamber it goes through the mitral valve to the left ventricle, and thence through the aorta being driven through the semilunar valves. The aorta gives off numerous arteries, which further divide many times and convey the blood to all the organs and parts of the body. The smallest arteries give off still smaller vessels called capillaries, and having a diameter hardly greater than that of a red corpuscle. It was in the capillaries of the web of the frog's foot that Harvey first demonstrated the fact that the blood circulates, and the observation may be repeated by anyone who examines this organ in a living frog with the low power under the microscope. The capillaries reunite together to form the veins through which the blood is conveyed back to the heart. The veins form an elaborate branching system resembling that of the arteries, the smallest veins being those formed by the junction of capillaries.

The arteries have thicker walls than the veins, and excepting the aorta and the pulmonary artery do not possess valves. The veins on the other hand may have valves which admit of the blood passing in the direction of the heart but not in the opposite direction. The wall of an artery consists typically of three coats, the inner consisting of elastic tissues lining the lumen, the middle of unstriated muscle fibres and the outer of fibrous tissues. The wall of a vein contains less muscular and elastic tissue but is otherwise not dissimilar to that of an artery.

The Lymph. A capillary has a still thinner wall than a vein, and through this wall the blood plasma transudes forming the lymph which is contained in the loose connective tissue and bathes the cells of the body. It is this intimate relation between the lymph and the tissues which admits of the process known as 'tissue respiration' (that is to say, the gaseous exchange between the tissues and the blood) and of nourishment being supplied from the blood to the tissues, and of waste products being removed. From the unenclosed spaces in the tissue the lymph is collected in thin-walled vessels which join together forming the lymphatics. These vessels, which like the veins may possess valves, communicate eventually with the thoracic duct or with the left lymphatic trunk which open into the large veins near the heart as already described at the end of the last chapter.

Placed in the course of the lymphatic vessels are the so-called lymphatic glands which consist of areolar tissue packed with lymphocytes. When in a position where the vessels connected with them are receiving lymph from an inflamed area these glands tend to become swollen and may cause a considerable amount of discomfort or pain. If owing to one cause or another (local obstruction of vessels or partial failure of the heart to discharge its functions through valvular disease) the lymph increases in the tissues to a quantity beyond the normal, a condition of oedema or dropsy is produced.

The Pulse. The alternate contraction and dilatation of the heart makes itself felt in the arteries as the pulse. When an artery is situated near the surface of the skin and there is a bony background present, the pulse or pressure wave produced by the heart beat can be recorded by an instrument known as a sphygmograph which is placed over the artery and responds to the varying pressure. A tracing can then be obtained by allowing a piece of smoked paper to pass across the recording needle of the instrument, the movements of the needle being regulated

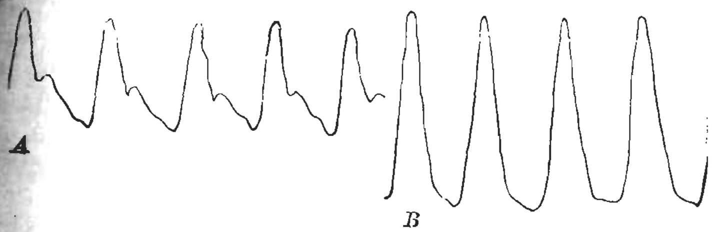


Fig. 35. Sphygmograph tracing from facial artery of horse (after Hamilton from Smith, Messrs Baillière, Tindall and Cox). *A* before and *B* after destruction of aortic valves; in *B* the dicrotic notch has disappeared.

by the beats of the pulse. A typical pulse tracing obtained in this way is shown in the figure. The straight upstroke represents the dilatation of the artery due to the increased blood pressure caused by the contraction of the heart. This is followed by a curved downstroke representing the period of arterial contraction, and this in turn is succeeded by another period of arterial expansion. The downstroke in the tracing is not a continuous curve, but is broken by a slight rise known as the dicrotic wave or notch. This has been shown to be due to the recoil of blood produced by the closure of the semilunar valves in the aorta, for in horses in which these valves have been destroyed experi-

mentally, there is no such recoil, the downstroke of the sphygmograph tracing being then continuous. In the veins there is normally no pulse.

The normal rate of the pulse (or of the heart beat) varies in different animals; it also varies under different conditions. Exercise increases the rate of the pulse, just as it increases the respiratory movements. The heart rate responds also to nervous excitement, and it quickens when there is a rise of temperature as in febrile conditions. The increased rate is apparently due to reflex stimulation, and in the case of fevers, the rise of temperature in the blood is probably the exciting cause. In young animals the rate is always faster than in adults, and with the advance of old age the pulsations become still slower and at the same time weaker. The following are the average rates for the heart beat in man and fully grown animals:

Man	72	beats per minute
Horse	38	,, ,, ,,
Ox	46	,, ,, ,,
Sheep	75	,, ,, ,,
Pig	75	,, ,, ,,
Dog	95	,, ,, ,,
Cat	130	,, ,, ,,

In the newly born foal or calf the average rate is about 110 beats per minute.

The velocity of the blood varies in the different parts of the body. In the carotid artery of the horse it has been shown to flow at the rate of 300 mm. per second (Volkmann). In the jugular vein of the dog it may flow at the rate of 260 mm. per second (Vierodt). In the smaller veins and arteries the rate of flow is much slower, and in the capillaries it is slowest of all, having been estimated at about an inch per minute. In no part of the body, however, does the blood traverse more than an extremely short distance through capillaries before being returned to a vein. Vierodt, by injecting potassium ferrocyanide into the jugular of a dog and awaiting its appearance at the other jugular, found that a complete circulation only took 16·32 seconds.

In the arteries the blood is kept in motion by the direct action of the heart. In the veins the flow is due to several causes. One of these is the back pressure due to the heart, but there are other contributing causes. Thus the expansion of the thorax in

breathing results in a suction of blood along the large veins entering the heart, and the compression of the diaphragm assists in driving the blood in the same direction. Moreover, the movements of the muscles involved in exercise exert pressure on the veins, and tend to drive the blood onwards, the action of the valves assisting. In the same kind of way muscular movements cause the lymph to flow along the lymphatic vessels which are also provided with valves. It is partly for this reason that exercise has a beneficial effect upon the circulation, and it is well known that horses whose legs have become swollen or oedematous through much standing may often be cured by moderate exercise

Blood Pressure. It is of course obvious that the blood is retained in the body under pressure. Thus, if we cut a large artery the blood flows out in a forcible stream and with spurts corresponding to the heart beats. Exact measurements of the degrees of pressure were first obtained by Hales who connected the femoral artery of a horse with a long glass tube in which the blood rose to a height of eight feet three inches and then remained approximately steady. This experiment showed that in the normal closed artery the blood was under a pressure or tension sufficient to support the weight of a column of blood (or water) to this height. He then performed a similar experiment with a large vein and found that the blood rose only to a height of one foot, showing that the blood pressure in the veins is very much less than in the arteries. Later experimenters have substituted a column of mercury for a column of blood, mercury being 13·5 times as heavy as blood (or water). Moreover, a manometer formed in this way may have its piston connected with a recording drum, and a permanent tracing of the variations in the blood pressure can be obtained.

The degree of arterial pressure is not due solely to the heart; it is also regulated by the action of the nerves supplying the arteries. These nerves are of two kinds. There are vaso-constrictor fibres belonging to the sympathetic system (on which the hormone adrenalin acts), and vaso-dilator fibres of different and diverse origin, which produce inhibition or temporary paralysis of the arterial muscles, and so cause the arteries to expand.

CHAPTER V

THE RESPIRATORY ORGANS

In the act of inspiration the air passes in through the nostrils (or sometimes through the open mouth) and traverses, first, part of the pharynx, and then the larynx and trachea before

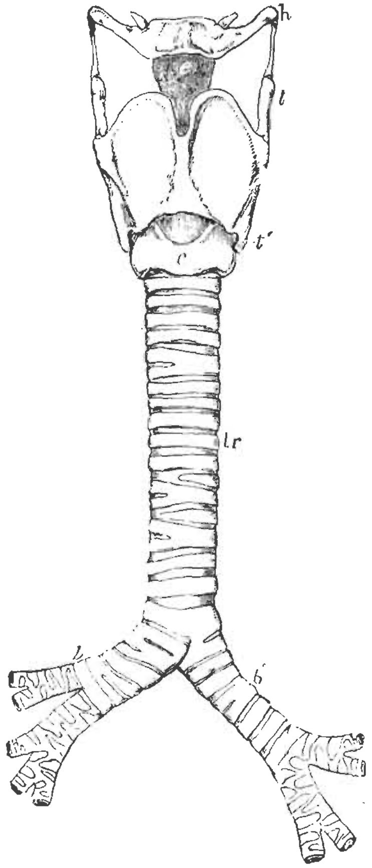


Fig. 36. Larynx, trachea and bronchi (after Allen Thomson, from Halliburton). *h* hyoid bone, *e* epiglottis, *t* and *t'* thyroid cartilage. *c* cricoid cartilage, *tr*. trachea, *b* and *b'* bronchi.

entering the lungs. The narrow slit-like opening from the pharynx into the larynx is called the glottis. The larynx is the enlarged first portion of the trachea. The latter organ which is commonly called the wind-pipe is kept open for the free passage of air by a number of rings of cartilage which are not quite complete. After reaching the thorax the trachea divides into the two bronchi which are provided with similar cartilaginous rings, and these bronchi after entering the lungs divide into smaller air tubes each of which in turn divides further into a

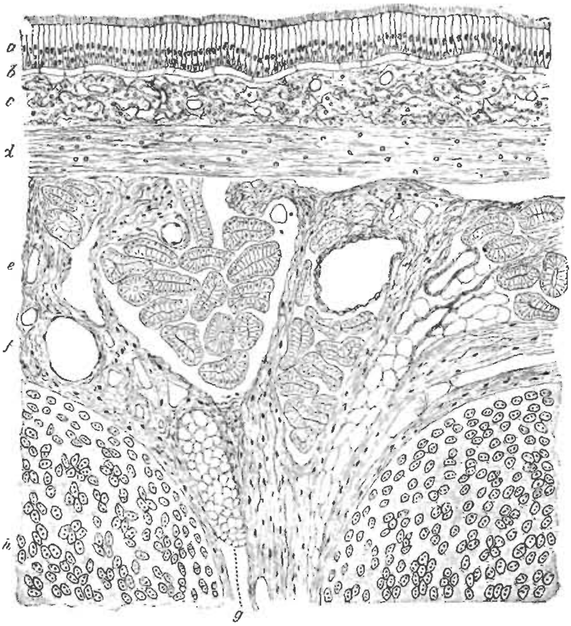


Fig. 37. Longitudinal section of trachea (after Klein, from Schafer). *a* ciliated epithelium, *b* basement membrane, *c* and *d* mucous membrane, the superficial part with vessels and lymphoid tissue, the deeper part with elastic tissue, *e* submucous areolar tissue containing glands, fat etc., *f* fibrous tissue, *g* adipose tissue, *h* cartilage.

number of bronchioles. In addition to the cartilaginous rings the walls of the trachea and bronchi contain some muscular and connective tissue and are lined internally by a ciliated epithelium. The bronchioles widen out into the air sacs of the lungs, which are arranged around the ends of the bronchioles like bunches of grapes. The walls of the air sacs are very thin, and are in

contact with innumerable capillaries which form a close meshwork. Thus these capillaries are separated from the air in the air sacs by the thinnest possible layer of protoplasm through which a gaseous exchange is effected. The result of the repeated branching and subdivision of the air tubes is to bring a very large surface of blood under the influence of the air in the air sacs of the lungs. In the human subject it is estimated that no less than 2000 square feet of blood surface is exposed to the air in this way.

In the act of expiration the air passes through the same passages as in inspiration but in the reverse direction.

Each lung is surrounded externally by a layer of fibrous tissue,

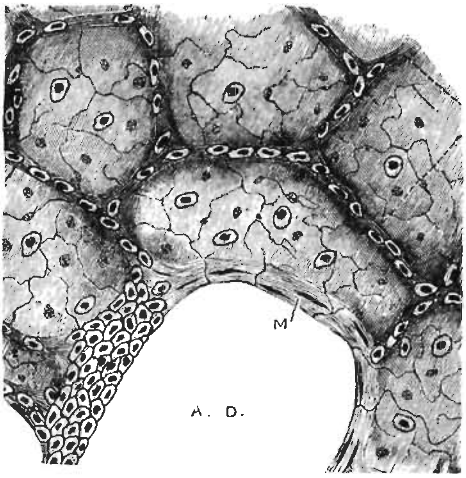


Fig. 38. Section through lung tissue (after Klein, etc., from Halliburton). *A D* alveolar duct. *S* septa. *N* alveoli or air-sacs. *M* unstriated muscle.

and the wall of the thoracic cavity is lined by a similar layer. Normally these two layers or pleurae are separated by only a very small quantity of serous fluid which however increases in amount in the inflammatory condition known as pleurisy.

Inspiration is brought about by the expansion of the thorax, the surfaces of the lungs continuing in contact with the pleurae and the pleurae with the thoracic wall. In this way the lungs are caused to expand, and air is drawn into them through the trachea in order to fill up the spaces which would otherwise occur. The thoracic movement involved in inspiration is produced by the contraction and consequent recession of the

diaphragm, and by the elevation of the ribs through the contraction of the intercostal muscles. In the reverse process of expiration the ribs are let fall to their former position and the diaphragm becomes extended again. Expiration requires little or no muscular effort.

The amount of air inspired in ordinary quiet breathing in man is about 500 c.c. (tidal air). By a forced inspiration another 1500 c.c. may be taken in (complemental air). Following upon an ordinary expiration an additional 1500 c.c. may be expelled by a forced expiration (supplemental air). The maximum amount of air which can be expelled after the deepest possible inspiration (i.e. tidal + complemental + supplemental air) is defined as the vital capacity. In man this quantity is on an average about 3500 c.c. (or from 3 to 3·8 litres). In the horse the vital capacity is from 25 to 30 litres. The air which remains in the lungs after a forced expiration (residual air) is about 1·5 litres for a man, or from 7 to 17 litres in a horse.

The number of respirations or breaths per minute varies in different animals, and as a general rule the smaller the animal the greater is the frequency. The following are average numbers for man and the domestic animals in a state of rest:

Man	14 to 18	per minute
Horse	8 to 10	,, ,,
Ox	12 to 15	,, ,,
Sheep	12 to 20	,, ,,
Pig	10 to 15	,, ,,
Dog	15 to 20	,, ,,

That the blood in the lungs absorbs oxygen and excretes waste carbonaceous matter in the form of carbon dioxide can be proved by various experiments. Thus, by comparing the composition of expired air with inspired air we get the following result:

	N	O	CO_2
Inspired air	79	20·96	·04
Expired air	79·4	16·50	4·10
		4·46	4·06

The total quantity of air expired is slightly less than that of air inspired since some of the oxygen taken instead of going to form carbon dioxide unites with hydrogen to form water. This accounts for the smaller percentage of nitrogen in the inspired air

We may also compare the relative amounts of the various gases in arterial and venous blood. For this purpose a mercurial gas pump is used; the blood is exposed to a vacuum and gas is thereby evolved and may be measured, potash being employed to absorb the carbon dioxide, and pyrogallic acid to absorb the oxygen. It is found in the case of both venous and arterial blood that 100 vols. of blood yield about 60 vols. of gas. This 60 vols. of gas is composed approximately as follows:

From the pulmonary artery		*From the pulmonary vein*	
O	12 vols.	O	20 vols.
CO_2	46 ,,	CO_2	38 ,,
N	2 ,,	N_2	2 ,,

The purpose of pulmonary respiration is to convert venous blood into arterial blood. The essential difference between these two kinds of blood depends, as has just been shown, on the relative quantities of oxygen and carbon dioxide which they each contain. The passage of these gases from or to the blood in the capillaries of the lungs is regulated normally by the pressure under which the respective gases are present in the air cells of the lungs. Thus oxygen is generally present in the air cells under a pressure of about 100 mm. of mercury, and this is quite sufficient to cause the venous blood to become arterialised. In the case of water the amount of oxygen (or any other gas) dissolved is proportional to the pressure to which the gas is subjected. If the pressure is doubled the amount of gas dissolved is also doubled. In the case of blood however this relation does not hold, since the quantity of oxygen in blood is *not* proportional to the pressure of the oxygen in the air to which the air is exposed through the thin lining of the air cells. This is because the oxygen is not merely in solution but is in chemical combination with the haemoglobin of the red corpuscles, forming oxyhaemoglobin. Consequently a given quantity of blood can absorb a much greater amount of oxygen than can the same quantity of water. The effect of a varying oxygen pressure on oxyhaemoglobin can be expressed in the form of a curve, called the dissociation curve of oxyhaemoglobin, and this curve varies under different conditions. Thus in an aqueous solution of haemoglobin the quantity of oxygen combining with it to form oxyhaemoglobin is very much greater owing to the absence of blood salts which make the compound less stable. Moreover, a rise in the temperature of the blood, or

an increase in the amount of carbon dioxide also favour dissociation. The carbon dioxide like the oxygen in the blood is not simply dissolved in the blood but is in this case in combination with the proteins in the blood plasma, with haemoglobin in the corpuscles as well as with sodium bicarbonate. The dissociation

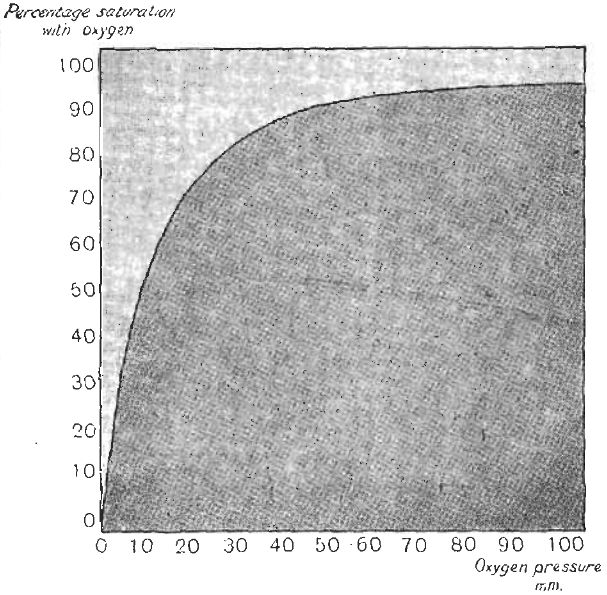


Fig. 39. Dissociation curve of oxyhaemoglobin (from Barcroft's *Respiratory Function of the Blood*).

curve of carbon dioxide in the blood is in general form similar to that of oxygen. About 2½ per cent. of carbon dioxide is dissolved in the blood and is not in a state of chemical combination with the salts or proteins.

Internal Respiration. In the tissues the arterialised blood becomes converted into venous blood, and the process whereby this occurs is termed internal or tissue respiration. Living tissues undergo a perpetual process of oxidation to a greater or less extent (according to the activities of the cells concerned), and consequently oxygen is being continually absorbed while carbon dioxide is produced and given off into the blood. When the tension of carbon dioxide in the blood increases beyond the normal it has a direct stimulating action upon the respiratory centre in the medulla oblongata and the movements involved in

breathing become deeper and *quicker*. This is what happens during physical exertion, but the condition can be produced by allowing an animal to breathe air containing an abnormal amount of carbon dioxide (2 to 3 per cent. Rumination also causes a slight increase in the respiratory movements in cattle and sheep). Laboured breathing due to excess of carbon dioxide is known as dyspnoea, and if continued may pass into asphyxia. On the other hand if the carbon dioxide tension falls below a certain level (as by *forced* breathing which removes an abnormal amount of the gas from the lungs and therefore from the blood) the respiratory movements are slowed or stopped for a time. This condition is known as apnoea.

The rate of the respiratory movements is influenced further by other acids than carbon dioxide, and in particular by lactic acid which is produced during muscular exercise; moreover a condition of acidosis which quickens the rate of movement occurs in certain diseases (*e.g.* diabetes, when oxybutyric or other organic acids may be present in the blood).

The respiratory movements are also affected by nervous influences, as by stimulating the vagus when the movements become quickened. If on the other hand the vagus is cut the movements become slowed. The same result is produced by stimulating the superior laryngeal nerve which therefore acts antagonistically to the main branch of the vagus. It is a familiar experience that the respiratory movements are affected by emotion or fright, and also that unlike the movements of the heart they are under the control of the will. The complete nervous mechanism is very complicated and only imperfectly understood. The efferent nerves concerned are the intercostal and the phrenic nerves, the former passing to the intercostal muscles and the latter to the diaphragm.

The Respiratory Quotient. Carbon dioxide contains its own volume of oxygen. Thus if carbon is burnt in air the volume of gas remains unchanged. Carbohydrates (e.g. $C_6H_{10}O_5$) contain sufficient oxygen to oxidise their hydrogen. Proteins on the other hand do not, and still less do fats. Consequently when proteins or fats are consumed in metabolism the carbon dioxide produced is less than the oxygen used: that is to say, oxygen has been employed to oxidise the hydrogen as well as the carbon. The following are the exact figures:

In the case of carbohydrate 1 vol. of O produces 1 vol. of CO_2.
In the case of protein 1 vol. of O produces ·83 of CO_2.
In the case of fat 1 vol. of O produces ·71 of CO_2.

The ratio $\frac{CO_2 \text{ produced}}{O_2 \text{ consumed}}$ is called the respiratory quotient. This in a man on an ordinary mixed diet is ·9 or somewhat less. It can be raised by increasing the relative amount of carbohydrate in the food, and lowered by protein or by fat. Thus the respiratory quotient is higher in herbivorous animals than in carnivorous ones. If a herbivorous animal be kept on carbohydrate diet its respiratory quotient may be raised to unity, but only for a short time, since it very soon begins to consume its own stored up proteins and fats.

CHAPTER VI

THE EXCRETORY ORGANS

When protein substances undergo decomposition or combustion they ordinarily yield ammonia together with sulphides or sulphates. But ammonia being a poisonous substance is not permitted to circulate freely in the body in any considerable quantity. The ammonia, therefore, which is produced as a result of the oxidation of proteins is converted into other substances which are innocuous. The principal of these is urea which is one of the principal constituents of normal urine. It is probably produced in the organism from ammonium carbonate which is itself formed from ammonia, carbon dioxide and water:

$$2NH_3 + CO_2 + H_2O = (NH_4)_2CO_3$$

and $$(NH_4)_2CO_3 = 2H_2O + CO(NH_2)_2.$$

Urine, the composition of which is described below, is excreted by the kidneys. These organs are of the nature of compound tubular glands and are situated dorsally on each side of the lumbar region of the vertebral column, the right kidney being placed in front or headwards of the left. The ureter or kidney duct issues from about the centre of the inner or concave surface of the kidney and conveys the urine to the bladder into the posterior side of which the two ducts open side by side not far from the opening of the bladder into the common urogenital passage. The latter communicates with the exterior in the male by the penis and in the female by the common vaginal opening.

To the naked eye the kidney (as seen in longitudinal section) appears to be formed of a cortical portion on the outside, and a medullary portion on the inside. The medullary portion surrounds the cavity or pelvis which is the dilated end of the ureter. Into the pelvis one or more conical processes project. These are called the papillae, and they contain the openings of excretory tubules into the pelvis. Each papilla really represents the apical part of a pyramid, for the medulla of the kidney in most

animals is divided into a number of pyramidal portions, the bases of which are surrounded by cortex. Both medulla and cortex are largely composed of uriniferous tubules, but the cortex contains more blood vessels and is consequently darker in appearance.

The tubules begin as Malpighian capsules and these are confined to the cortex. Each capsule has projecting into it a bunch of coiled capillaries called a glomerulus, and the blood

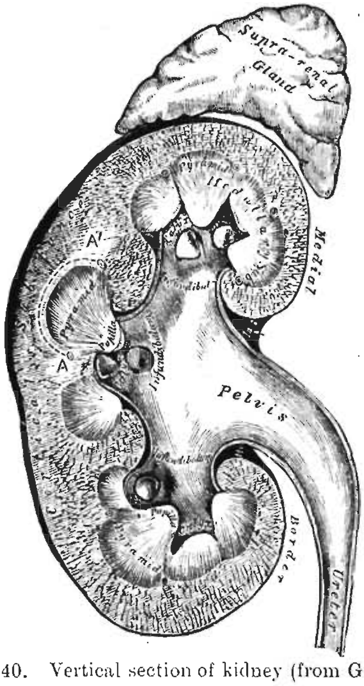


Fig. 40. Vertical section of kidney (from Gray).

enters these capillaries by a small artery and leaves them by a small vein.

Each tubule as it leaves its dilated end or Malpighian capsule becomes convoluted, passing through the medulla in the direction of the apex of the pyramid, and then back again to the cortex. The loop which is thereby constituted is known as the loop of Henle. In the cortex the tubule again becomes convoluted and then after uniting with other tubules passes straight to the papilla. The tubules are lined throughout by an epithelium which varies in character in their different parts. The cells

lining the convoluted tubules and those of the ascending limb of the loop of Henle are granular and striated and generally large, while those of the collecting tubules and the descending limb of the loop of Henle are cubical and free from granules.

The Mechanism of Renal Secretion. There appear to be two main factors in the secretion of urine, (1) the supply of blood, and (2) the composition of the blood flowing through the kidney. There are no secretory nerves going to the kidney.

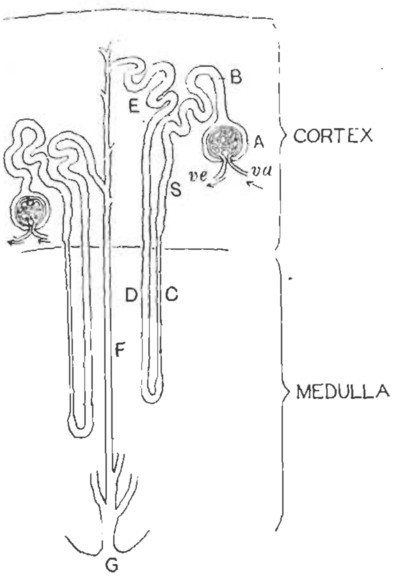


Fig. 41. Diagrammatic view of the course of the tubules in the kidney. A, Malpighian capsule containing a glomerulus; B, first convoluted portion of tubule; C, descending limb of loop of Henle; D, ascending limb of loop of Henle; E, second convoluted portion; F, collecting tubule; G, apex of pyramid; S, spiral tubule; *va* represents a small branch of the renal artery, which breaks up into a bunch of looped capillaries, the glomerulus finally joining up again to form the vein *ve*.

That the secretion of urine is affected by the blood supply to the kidney is rendered obvious when we consider the result of different degrees of temperature upon the skin. Cold causes a constriction of the vessels in the skin and consequently lessens the supply of blood to the skin, while the supply going to the kidney is correspondingly increased. Conversely when the skin is hot and flushed, and when evaporation of moisture from the

skin is considerable the quantity of urine secreted is diminished. Just as the vessels in the skin are under the influence of vaso-constrictor nerve fibres which react to external cold, so also the vessels supplying the kidneys are controlled by nerve fibres which regulate the supply of blood and the consequent secretion of urine. Thus if the renal nerves are cut, the renal arteries dilate, and the flow of urine increases. On the other hand, if the renal nerves are stimulated the vessels are constricted, and urinary secretion is diminished.

It is believed that the glomeruli act somewhat after the manner of a filter and allow the water and salts of the blood plasma to pass through. At the same time the cells of the kidney have the definite property of picking out certain substances from the blood and permitting these to be excreted while other substances (e.g. the proteins in solution in the blood) are not normally allowed to pass through. Further, it has been established that certain substances (e.g. pigments such as indigo carmine, and probably some of the substances present in normal urine) are excreted by the epithelial cells lining the convoluted tubules and not by the glomeruli.

Certain substances known as diuretics promote urinary secretion within a very short time after they are taken into the system, probably through their action on the nerve fibres supplying the renal vessels. Thus it is well known that alcohol and various drugs have such an action, and that tea, coffee, etc. contain diuretic substances.

The urine is driven along the ureters into the bladder largely as the result of pressure by quantity. The ureters are lined by a stratified epithelium surrounded by unstriated muscle which assists in the passage of the urine into the bladder. The walls of the latter organ also contain an abundant supply of unstriated muscle (lined internally by a stratified epithelium). Around the neck of the bladder is a sphincter which is kept contracted excepting during micturition or the evacuation of urine. During micturition the sphincter relaxes, while the walls of the bladder contract. The abdominal muscles also contract, and in the male the perineal muscles. Normally in animals micturition is a reflex act presided over by a centre in the lumbar part of the spinal cord, the accumulation of urine in the bladder being the necessary stimulus for inducing the reflex. In man, however, and

to some extent in animals, micturition (like defaecation) may be a voluntary act, that is to say, it is possible to inhibit the reflex which would otherwise occur.

A horse during micturition stands with its hind-legs extended, its fore-legs generally advanced, and its tail raised upwards. After micturition the mare erects the clitoris, but why this should happen is not obvious. Horses as a rule can only micturate when standing upright. They cannot do so while lying down, or while at work or trotting, but an oestrous mare can discharge urine while cantering. In the ox micturition can occur while walking. The cow raises her back and brings her hind limbs forward, at the same time lifting her tail.

The following are the daily amounts of urine discharged in man and the domestic animals under normal conditions:

Man	1·5 litres
Horse	5 to 8 litres
Ox	10 to 25 ,,
Sheep	1 to 5 ,,
Pig	1·5 to 8 ,,
Dog	·5 to 3 ,,

It will be seen that the amounts given for any one species show a wide range of variation. This is due partly to differences in the size of the animal, but to a greater extent to the influence of temperature variation and the factors referred to above.

Composition of Urine. Normal urine may contain the following substances:

(1) Water.
(2) Nitrogenous end products (urea, uric acid, hippuric acid, creatine, creatinine).
(3) Aromatic compounds (benzoic acid, ethereal sulphates of indol, etc.).
(4) Mucus.
(5) Colouring matter.
(6) Inorganic salts (chlorides, sulphates and phosphates of sodium, potassium, calcium and magnesium).
(7) Gases (chiefly carbon dioxide, and traces of nitrogen and oxygen).
(8) Ammonia.

We may now consider these separately and then pass on to deal with certain features of special interest in the urine of the different domestic animals.

Urea. $CO\begin{matrix}\diagup NH_2 \\ \diagdown NH_2\end{matrix}$ is a substance which readily crystallises into four-sided prisms or indefinitely shaped prisms. With nitric or oxalic acids it forms characteristic crystalline salts. It is soluble in water and alcohol and neutral in reaction. Under the influence of organised ferments (due to *Micrococcus ureae* or other bacteria) it takes up water and forms ammonium carbonate $(NH_4)_2CO_3$; hence the ammoniacal odour of putrid urine. The amount of urea present in a given sample of urine can be estimated by making use of the following equation:

$$CO(NH_2) + 3NaBrO = CO_2 + N_2 + 2H_2O + 3NaBr.$$

The sodium hypobromite solution also contains soda (if not some soda should be added) and this absorbs the whole of the carbon dioxide evolved. The nitrogen therefore is the only gas given off, and this on being measured gives a basis for estimating the original quantity of urea present. The urine of man and that of the horse contain about three per cent. of urea; that of the ox contains one and a half per cent., whereas the pig's urine contains less than one per cent.

Urea is produced in the liver and not in the kidneys which merely excrete it. Thus after extirpation of the kidneys the quantity of urea in the circulation is greatly increased. If ammonium carbonate is given by the mouth the urea output is also increased. The portal vein which conveys blood to the liver contains more ammonia than the hepatic vein which drains the liver. If however the portal vein is ligatured or united artificially with the vena cava the quantity of ammonia in the blood is raised. After removal of the liver in frogs urea formation almost ceases and ammonia is found in the urine instead. Moreover when the kidneys are diseased in a certain way urea is still formed in the body but cannot be excreted and we get the condition known as uraemia. On the other hand when degenerative changes occur in the liver urea formation is lessened, and in acute yellow atrophy may scarcely be produced at all.

Uric acid, ($C_5H_4N_4O_3$ tri-oxypurine), crystallises in rectangular prisms. It does not occur free in urine but combined with bases (sodium and potassium) to form urates. The amount of uric acid in urine may be estimated by adding ammonium chloride;

ammonium urate is produced and is dissolved in an alkaline solution. Hydrochloric acid is then added and uric acid is precipitated and can be weighed directly (Hopkins' method).

From a chemical standpoint, uric acid is a member of a group of bodies called *purines*, all of which are characterised by the presence of a ring compound called purine ($C_6H_5N_4$). The chief physiological compounds representative of this group are adenine and guanine, xanthine, hypoxanthine and uric acid. The active constituents of tea, coffee and cocoa are the methyl purines caffine, theine and theobromine. Adenine and guanine are constituents of the nucleic acid contained in cell nuclei, and by means of ferments these bodies are oxidised to hypoxanthine ($C_6H_5N_4O$) and xanthine ($C_6H_5N_4O_2$). Further oxidation of hypoxanthine and xanthine gives rise to uric acid.

Uric acid is found only in small quantity in the urine of herbivorous animals, and in the healthy horse it is altogether absent. In Carnivora it is abundant and it is the principal nitrogenous constituent of the excretory products of birds and reptiles. In man it is present, and frequently to an extent which is pathological. The amount depends on the diet, and meat eating always favours uric acid production. It is present in all young animals which are living on their mother's milk, and in herbivorous animals which are being starved or are in a state of fever since these are for the time being living on their own tissue and are therefore temporarily carnivorous. Like urea, uric acid is not manufactured by the kidneys, since after the removal of these organs it is still produced. In birds uric acid is formed in the liver and ceases to be excreted if the liver is excised. In mammals, however, its origin is more complicated, but there can be little doubt that the liver and spleen are responsible for much of its formation. Certain kinds of food which contain a large quantity of nucleic material (e.g. liver and pancreas which possess many nuclei, and to a greater or less extent meat generally) are known to be very rich in purine bases, and these are converted into uric acid through the action of ferments. Such ferments which are termed nucleases are most abundant in the liver and spleen. It follows from what has been said that uric acid may be formed, partly as a result of eating food which is rich in nuclei or purine bases (exogenous formation), and partly in metabolism from the nuclei of the

various organs and tissues (endogenous formation). The former mode of *production* is largely responsible for those disorders (e.g. gout) which are due to excess of uric acid, and such disorders may be palliated or cured by restricting the diet (as by avoiding meat which is especially rich in the purine base hypoxanthine, $C_5H_4N_4O$).

Hippuric acid, ($C_6H_5CO.NH.CH_2COOH$ benzoyl glycocoll), is especially characteristic of the urine of Herbivora in which it is present in the form of hippurate salts. It may be crystallised out from horse's urine by evaporating to a syrup and saturating with hydrochloric acid. As its formula suggests, it orginates through the combination of benzoic acid (C_6H_5COOH) and glycocoll (CH_2NH_2COOH) with the elimination of water. This synthesis occurs in the kidney itself, and is possibly due to the action of a ferment. This is rendered probable by the fact that benzoic acid and glycocoll can be made to unite to form hippuric acid in the presence of ground up kidney extract mixed with blood. There is a hippuric acid forming substance in hay, grass and grains.

Benzoic acid, (C_6H_5COOH), is said to be present in the urine of working horses, and as has been stated it is a precursor of hippuric acid. Benzoic acid is apparently derived from various aromatic substances which are present in plants and are absorbed in the food.

Creatine, ($C_4H_9N_3O_2$ methyl guanidine acetic acid), is a constituent of muscle and is not found in urine excepting during starvation, and in certain febrile and other pathological conditions.

Creatinine, ($C_4H_7N_3O$), which is the anhydride of creatine is present in normal urine and in generally constant amount. There is evidence that the liver is the chief seat of its formation. It is a product of protein metabolism, and according to Mellanby probably gives rise to the creatine of the muscles, any excess of creatinine, which is not required for this purpose, being excreted by the kidneys.

Indican. Of the ethereal sulphates occurring in the urine phenyl sulphate of potassium and indoxyl sulphate of potassium are chief. The latter is formed from indol potassium hydrogen sulphate. Indol is a product of intestinal disintegration produced from tryptophane by bacterial putrefaction. It is not normal in human urine, though it very frequently occurs, but it

is always present in the urine of the horse and many other Herbivora. It may be made to yield indigo.

Mucus. The urine of the horse is generally more or less mucinous, the amount of mucus depending upon diet, the occurrence of oestrus, etc. On a diet of oats without hay the quantity may be considerable. Mucus in small amounts is often present in the urine of other animals.

Pigments. The chief colouring matter of urine is urochrome, an oxidation product (on exposure to air) of urobilin which is a derivative of bile-pigment.

Salts. These are derived partly from the salts of the food, but to a greater extent are metabolic products of the tissues. They are always present in considerable quantity, but vary in kind according to diet and according to the species of animal.

Gases. The gases in urine only occur in insignificant quantities.

Ammonia. Urine always contains a small quantity of ammonia since blood containing this substance traverses the kidney before reaching the liver where it is converted into urea.

Pathological constituents of urine. Protein is present in human urine in cases of Bright's disease (albuminuria) and in certain other pathological conditions, especially when pus is formed through bacterial action. Protein occurs in horse's urine in cases of inflammation of the lungs and pleura. In cases of glycosuria where the tissues are unable to utilise the sugar in the blood glucose overflows into the urine. Such a condition may be produced experimentally by removing the pancreas (see p. 141), by puncturing the floor of the fourth ventricle of the brain, or by injecting adrenaline, phloridzin and certain other drugs. In lactating animals lactose may occur in the urine. Sugar is rarely or never present in horse's urine. Bile occurs in urine in cases of jaundice, rendering the fluid a dark brown colour. Blood appears in the urine when haemorrhage in any of the urinary passages takes place. Further, a blood pigment (methaemoglobin) is found in cases of haemoglobinuria which is due to a disintegration of corpuscles in the circulating blood. In cattle with 'black water fever' (a disease of Tropical Africa) this pigment may also occur in urine associated with oxyhaemoglobin. Amino-acids, such as tyrosine, are occasionally found in urine after a disintegration of protein tissue (as in atrophy of the liver).

The urine of the horse has normally a specific gravity of about 1·036 (that of man being about 1·020). In colour horses' urine is yellowish-brown, rapidly becoming brown on standing. It is always turbid (owing to suspended calcium and magnesium carbonates). Its odour is due to aromatic substances. Indican and hippuric acid are well-marked constituents, the latter taking the place of uric acid. Phosphates are absent or only present in small amounts. The quantity secreted depends upon the season, the diet, and the amount of work done. On a nitrogenous diet the amount of water in the urine is greater; on a diet of oats and no hay the mucinous substances are more numerous and may be so much so that the urine has the consistency of egg albumin. In winter owing to the effect of cold on the skin the quantity of urine is greater than in summer. For a similar kind of reason horses at work secrete less than horses at rest. The urine of mares during oestrus may have the consistency of oil.

The urine of the ox has a specific gravity of about 1·015, being less than that of the horse owing to the greater amount of water secreted. The nitrogenous content consists chiefly of urea and hippuric acid but there is less of the latter than in the horse. Straw of cereals produces a large amount of hippuric acid, and when this is so the amount of urea is correspondingly less. Calves while sucking yield a urine in which phosphates and uric acid are abundant, such animals resembling Carnivora.

The urine of the sheep has a specific gravity of about 1·010. Hippuric acid is abundant, being produced especially by a diet of new meadow hay.

The urine of the pig has a specific gravity of about 1·015. Its composition varies with the diet, pigs being comparatively speaking omnivorous. Uric and hippuric acids are both important constituents, and there is also much urea.

The urine of the dog has a specific gravity of about 1·030, but it varies within wide limits. Uric acid is present typically, but is absent on a herbivorous diet. On a normal flesh diet the reaction is very acid (owing to acid sodium phosphate resulting from oxidation of the phosphorus of proteins in the meat). Indican is usually present.

CHAPTER VII

THE FUNCTIONS OF THE SKIN

The skin is composed of two main parts, the epidermis and dermis. The epidermis is subdivided into the cuticle or stratum corneum and the rete mucosum or Malpighian layer. Neither part of the epidermis contains any blood vessels.

The cuticular part consists of a stratified epithelium which is being continually given off in flakes. It is hard and horny. The rete mucosum is soft and protoplasmic, its cells frequently containing pigment (as in the coloured races of mankind). Intercellular channels conveying lymph are found in both parts of the epidermis but especially in the rete mucosum.

The dermis or cutis vera is a dense connective tissue containing numerous blood vessels. Its surface adjoining the epidermis is raised into little more or less rounded elevations called the papillae. These often contain sensory end organs (tactile corpuscles). Adipose tissue, sweat glands, and the roots of the hair are also present in the dermis in greater or less profusion.

The hair. A hair consists of horny epithelial cells. The part of it below the surface of the skin is enclosed in a kind of sac or follicle. At the bottom of this sac is the vascular papilla in which the newest portion of the hair develops. The shaft of the hair is developed by the epidermal cells surrounding the papilla becoming converted into horn. The cornified hair cells formed in this way are continually pushed outwards by fresh cells developed from below and the shaft of the hair consequently comes to protrude from the surface. When the hair is fully grown a new hair may arise by budding from the old pápilla and sac. The walls of the sac or follicle form the root-sheaths and are composed of epidermal and dermal cells which dip down from the surface, so as to enclose the hair root. The follicle, papilla and root-sheath are provided with nerve fibres, especially well-developed in large tactile hairs (whiskers). The hair shaft (i.e. the hair itself) is composed of a medulla or pith of loose texture

and frequently containing air spaces, and a cortex which surrounds the medullary portion, and generally contains pigment giving the hair its peculiar colour. With the advance of age this pigment is often removed by the action of phagocytes. Outside of the cortex is a thin cuticle formed of flat horny plate-like structures.

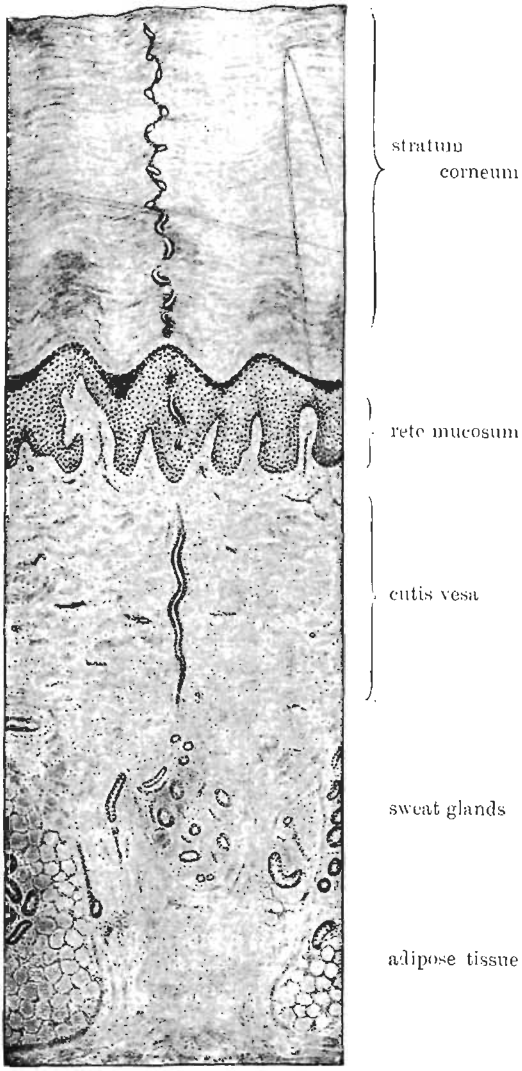


Fig. 42. Vertical section through skin of sole of foot (from Schafer).

The use of hair is to assist in heat retention. For this reason animals which are subjected to severe climatic conditions have thicker coats than those in warm countries. With horses the thickness of the hair varies with the breed, and the better bred the animal the finer the coat. There are about 4300 hairs to

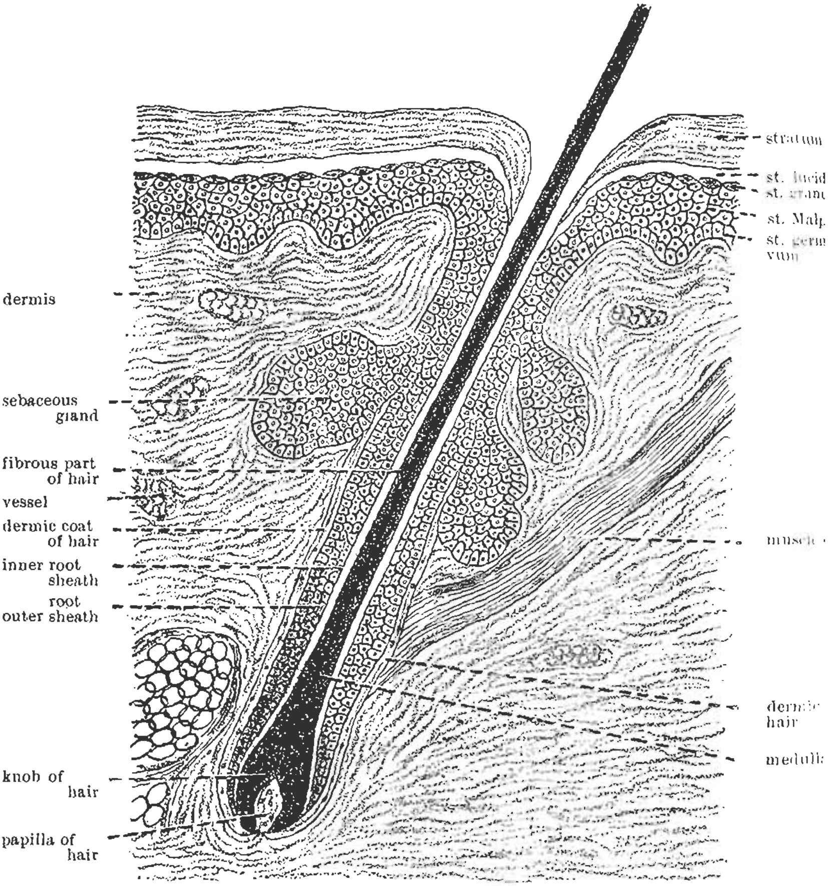


Fig. 43. Section of epidermis and dermis (from Gray).

a square inch excepting on the muzzle and lips, the inside of the ears, the inside of the thigh, the mammary glands and the external generative organs where there are very few hairs. The coat is changed twice a year, being alternately fine and thick. Generally speaking this change is related to the temperature of the air, and is not simply seasonal. Thus horses in a heated

atmosphere (such as a horse deck on board ship) may shed their winter coat in a few days although the outside temperature may be below freezing: similarly if taken to a cold locality from

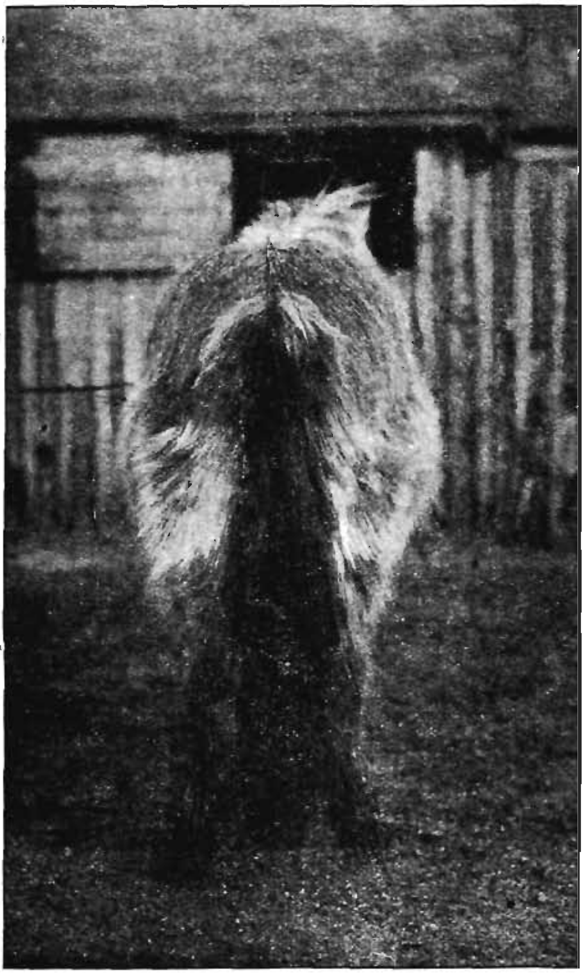


Fig. 44. Icelandic pony showing 'tail-lock' (from Ewart).

a warm climate the hair responds by growing longer. There are however temporary exceptions to this rule for horses after crossing the Equator may take a year before adjusting the length of their coat to the changed conditions. There are some

hairs which grow permanently, not being shed at recurrent periods. Such are the hairs of the mane and tail (with some exceptions), the eyelashes, and the long tactile hairs on the muzzle. The comparatively short hairs of the upper part of the tail (i.e. those forming the tail-lock) in Icelandic ponies and other ponies of the Celtic type are shed at the beginning of summer and regrown at the commencement of the following cold season. These hairs, as Ewart has pointed out, serve the purpose of protecting the anal region from snow which collects upon the upper surface of the tail-lock. It is well known that clipping or cutting has a stimulating effect upon hairs, causing them to grow longer. In some animals there are muscles attached to the hair roots, the function of which is to ruffle the hairs and so diminish the conduction of heat. Similar muscles are connected with the feathers of birds.

The hairs of various kinds of animals present considerable differences. Thus the hairs in deer are composed almost entirely of medulla; those in pigs consist largely of horny substance; while hair which has the property of mutual cohesion or 'felting,' depending upon a rough scaly surface and a disposition to curl, is characteristic of the sheep, being commonly called 'wool.'

Nails and claws like hairs are formed from the corneous cells of the epidermis which instead of being thrown off as flakes are consolidated to form horny structures. Underneath the nail is the vascular nail bed which is a modified part of the dermis thrown up into parallel ridges. The hoofs of Ungulates (described below in the chapter dealing with the organs of locomotion) have a similar origin to nails, being developed from horny epidermal elements fitting on to a modified dermis. The horns of cattle and sheep consist of bony processes ensheathed in a case of true horn which like the structures mentioned above is of epidermal origin.

Sweat glands. Over most parts of the epidermis in man and in the horse but confined to more or less restricted areas in certain other animals (see p. 91) are numerous pores which represent the openings of the ducts of the sweat glands. These ducts convey the secretions of the glands to the surface of the skin, and in so doing they traverse a portion of the dermis and the whole of the epidermis. The actual glands are situated in the dermis and consist of coiled tubes surrounded by a network of

capillaries not unlike the glomeruli of the kidneys. The secretion (sweat or perspiration) contains protein, fat, salts and water and is alkaline in reaction.

Sebaceous glands. Sebum is the greasy material secreted by the sebaceous glands. These lie alongside of the hairs and communicate by short ducts with the hair follicles. The secretion lubricates the hairs, and in horses gives gloss to the groomed coat. It also helps to keep off wet.

Dandruff, which is the material removed in grooming a horse, consists of epithelial scales, fat, sebum, etc.

The functions of the skin are five in number:

(1) Protective.
(2) Sensory.
(3) Respiratory.
(4) Absorptive.
(5) Heat-regulating.

(1) The skin supplies a strong elastic coating for the body. It is thickest at places where injury is most frequent.

(2) The skin is an organ of touch being highly endowed with sensory nerve endings, especially in certain parts (e.g. the region of the external generative organs).

(3) The respiratory function is practically negligible in mammals and birds, but in some lower Vertebrata it is well developed. Thus frogs can live by breathing through their skin after the complete removal of the lungs.

(4) The skin's capacity for absorption is very slow in mammals though it definitely exists. Colin kept the lumbar region of a horse wet with a solution of potassium ferrocyanide and found traces of the salt in the urine after 4½ hours. The ill-effects of varnish on the skin are not owing to absorption, but are due to the fact that the varnish causes the capillaries to dilate and so produces an undue loss of heat.

(5) The heat-regulating mechanism possessed by the skin of all 'warm-blooded' animals is of very great importance. It is well known that in mammals and birds the temperature of the body is generally warmer than that of the surrounding air. Moreover, under normal conditions it keeps approximately constant, notwithstanding the varying temperatures to which the animal is exposed. This fact is implied in the term homoiothermal, which is applied to such animals. On the other hand

in poikilothermal or so-called 'cold-blooded' animals (e.g. reptiles and amphibians) the temperature of the body is roughly speaking the same as that of the outside air and varies with it. In hibernating animals (e.g. hedgehogs) there is a marked fall in the body temperature during the period of hibernation when the animal is in a state of deep sleep and complete inactivity.

The average normal temperatures in man and the domestic animals are as follows:

Man	98·4° F.
Horse	100·5° F.
Ox	100–102° F.
Sheep	103° F.
Pig	103° F.
Dog	101° F.

These are the temperatures at or near the surface. In the centre of the body the temperature is slightly higher.

It is evident that since heat production is always going on *in the body there must be a corresponding heat loss if the temperature* is to keep constant. It has been estimated that a horse produces sufficient heat during rest to raise the temperature to boiling point in less than two days. The heat loss which prevents such a rise of temperature is regulated by certain special mechanisms in the skin.

The muscles are the chief seat of heat production. They make up half or more than half of the body weight. During rest the oxidation processes which give rise to heat are always going on, and during activity the output of heat is still greater, as can be proved directly by observing that the temperature of a muscle rises as a consequence of contracting. Besides the muscles, however, heat production is associated with oxidation in all the organs, and the liver and other glands are sources of much bodily heat.

This constant production is compensated for by evaporation, radiation and conduction which takes place over the surface of the skin. The warmer the surface the greater is the heat loss, and the more blood going to the surface, the greater the warmth of the surface. The quantity of blood going to the surface is regulated by the nervous system. Thus when the surrounding air is warm, or when the bodily heat is increased by muscular exertion, the skin becomes hot and the vessels are dilated. The

converse happens when the temperature is cold and the body is at rest; then the surface vessels become constricted and the heat loss is greatly reduced.

If however the external temperature is very high or exercise is severe no amount of dilatation of vessels is sufficient to produce the necessary heat loss, and then another regulating mechanism comes into play, and this is the secretion of sweat. The moisture generally evaporates quickly unless formed too fast. It is a means of losing bodily heat. The secreting process is essentially a nerve reflex, and as in the case of the salivary glands may be antagonised by administering atropine. Moreover, by stimulating certain nerves electrically, sweat secretion can be increased (e.g. by stimulating the sciatic nerve in the dog when the sweat glands of the foot-pad secrete profusely).

There is experimental evidence of the existence of a centre in the fore brain which presides over and coordinates all the functional activities concerned with both heat production and heat loss.

As already mentioned there is a compensating action between sweating and the secretion of urine, these two processes being inversely proportional in their respective activities. Furthermore, the sweat glands besides supplying a heat-regulating mechanism are definite organs of excretion.

The horse is the only hairy animal which sweats easily from nearly every part of the body. A horse begins to perspire at the bases of the ears, the neck, chest and back follow, and finally the hindquarters. Sweating does not take place on the legs. With donkeys and mules sweating is confined chiefly to the bases of the ears. Oxen sweat mainly on the muzzle, and only with some difficulty elsewhere. Sheep also perspire very little, the number of sweat glands being relatively few. In pigs sweating only takes place on the snout. Dogs and cats can sweat profusely on the muzzle and foot-pads, but not on the general surface of the body. A dog when heated by exertion pants and throws out its tongue thereby admitting of an increased conduction of heat, but the glands inside the mouth are not sweat glands.

The fact that oxen and many other animals possess comparatively few sweat glands and do not perspire freely on the body explains the much greater range of body temperature which these animals normally possess. They cannot undergo

prolonged exertion without getting into a condition of distress, whereas a horse can gallop for miles. This is a point of some importance when we consider the usual method of applying the tuberculin test to cattle. Before injecting the tuberculin, the temperature of the animal is taken frequently on several successive days (but very often in practice on only one day). It is again taken after injecting, and a rise of 2·5° F. consequent upon it is regarded as denoting a reaction (that is to say, that the animal is affected with tuberculosis which augmented by the tuberculin injected causes a rise of temperature). It should be remembered however in the light of what has just been stated that the rise of temperature in animals so susceptible as cattle, may be due to other and quite different causes, such as excitement or the periodic occurrence of oestrus, and that a rise apparently associated with an injection may be a coincidence. Furthermore, the initial temperatures taken before an injection may be abnormally high owing to the same or similar causes, and a genuinely tuberculous condition may pass unnoticed owing to there being little appreciable rise of temperature following upon the injection.

It is well known that moisture present in cold air assists in heat conduction but that moisture in warm air hinders evaporation. This is why a hot dry climate is so much less trying than a hot moist one. In warm, moist, tropical climates it is difficult for the heat-regulating mechanisms to cope with the extreme conditions.

Clipping or shearing is liable to throw a severe strain on the heat-regulating apparatus, especially in cold moist weather. For this reason a shepherd cannot be too careful not to shear his sheep when the weather is unfavourable. On the other hand, in very woolly or fat animals the accumulation of heat may be such as to constitute a source of danger.

It is interesting to note that in the pig the fat in the dermis is normally well developed, for the pig has few hairs to withstand the conduction of heat.

In addition to the heat regulating mechanisms described above there is some evidence that heat production within the body is regulated by the outside temperature. Thus animals which are exposed to cold tend to eat more, and so a greater quantity of food is available for heat production. Starvation produces a lowering of the temperature of the body, and the absorption of

food raises it. Cold is least well stood by small lean animals, since in them the surface of the body is greater relative to their weight than in larger animals.

The rise of temperature which occurs during fevers is due partly to a defective dissipation of heat, the regulating mechanisms of the skin being deranged. Thus the skin surface is unusually dry and hot. Nevertheless, there is frequently also a great increase in the amount of heat actually produced during fevers, since the quantity dissipated may largely exceed the normal.

Cold perspiration is a pathological phenomenon and is apparently due to derangement of the nerves supplying the glands. It is unaccompanied by dilatation of the vessels. Disordered sweating is often associated with nervous affections.

CHAPTER VIII

THE NERVOUS SYSTEM

Every 'nerve' or nerve-trunk is composed of a number of fibres arranged in bundles and separated by connective tissue. The functional part of the nerve fibre is called the axon, and this in medullated nerves is surrounded by an insulated jacket composed of phosphorised fat and called the medulla or myelin. The

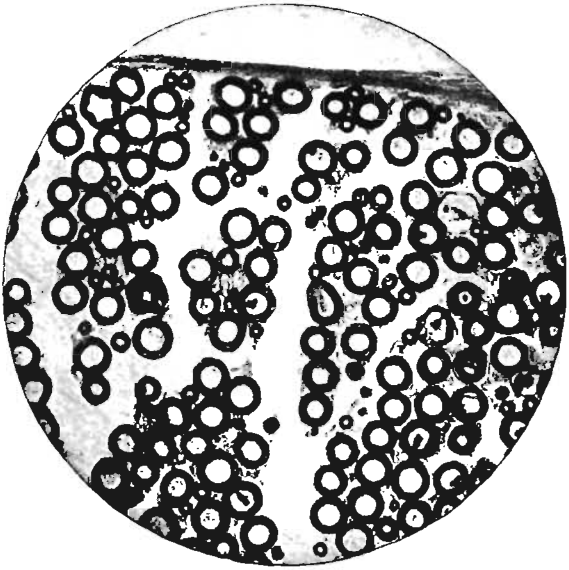


Fig. 45. Section through sciatic nerve of cat showing constituent fibres of different sizes (from Schafer).

medulla is broken at certain intervals to admit of the passage of nutriment to the axon from the tissue outside. The axons are extensions of nerve cells, and a nerve cell may have a number of such extensions. The name 'neuron' is given to a nerve cell together with all its extending axons, and the whole of the nervous system is composed of vast numbers of neurons.

The function of an axon is to convey a nerve impulse. The precise nature of such an impulse is still very obscure, but it appears to be a reversible physico-chemical process unassociated, so far as is known, with metabolic change. An impulse may be started artificially (as by stimulating with an electric current) at any part of a neuron, and if this is done it travels to every other part of the neuron. In normal life the impulse is started at one end of the neuron (being transmitted from the adjoining neuron), and travels to the other end, but in the case of accidents it may start at any point. Some slight expenditure of energy is required to set it up at the stimulated spot, but when once this is done, if the stimulus is sufficiently strong, it causes a propagated disturbance without being attended by any consumption or evolution of energy.

It is known that a nerve impulse is accompanied by an electrical change in the neuron concerned, and by taking advantage of this fact, the rate of transmission of an impulse can be measured. A stimulus is applied at one end of a long nerve, and the electrical condition of the nerve is recorded by a galvanometer at the other end. In this way it has been found that an impulse travels at the rate of twenty feet per second.

When an axon is cut the part still connected with the cell survives, the severed portion alone undergoing degenerative changes, the subsequent observation of which may serve as a guide to the destination of particular fibres.

The nervous system is composed of (1) the brain and spinal cord (together constituting the central nervous system), and (2) all the other nerves of the body, these forming collectively the peripheral nervous system. Impulses are of two principal kinds, those passing into the central nervous system (or afferent impulses) and those passing out (or efferent impulses). These two chief kinds of impulses are never transmitted along the same neurons.

An afferent or sensory impulse starts at some special sense organ and is conveyed along a neuron, whose nerve cell is small and placed in a ganglion (a collection of nerve cells) outside of but not far from the brain or spinal cord. The particular impulses differ from one another in that each starts from a different position and is carried to its own special destination in the central nervous system. The skin is full of such end organs, and

an impulse started in any one of them is different (though it may be only very slightly different) from an impulse started in any of the others.

The sensory end organs, the more important of which are described in the next chapter, may here be tabulated:

(1) End organs in the skin setting up impulses either on the application of pressure, or on being warmed or cooled.

(2) End organs in muscles, tendons, and ligaments, starting impulses when these are extended or contracted.

(3) The eye.

(4) The ear.

(5) The semicircular canals of the ear, which serve the purpose of balancing organs, owing to their containing water capable of running in three directions in a system of tubes, according to the position in which the head is held.

(6) The nasal organ (organ of smell).

(7) The mouth (taste organs).

(8) End organs which start impulses when neighbouring tissue is destroyed, the impulses conveying the sensation of pain which must be regarded as a warning of the existence of danger.

(9) Special end organs starting sensations peculiar to themselves (e.g. in the rectum, when full of faeces and calling for the act of defaecation).

The impulses which enter the central nervous system pass up and down through many neurons, the direction that they take being determined partly by congenital tendency and partly as a result of previous impulses which acted on the nerve cells through which they passed; that is to say, the direction of a nerve impulse may be affected both by heredity and by education or training. and a nerve reflex may be established in either of these ways.

An impulse can pass from one neuron to the next in one direction only. This is because the synapse or region where two neurons join has a valve-like action.

The efferent nerves by which the impulses leave the central nervous system are of two kinds. Firstly, there are axons which innervate voluntary or striated muscle (the movement of which is under the control of the will). Such nerve fibres pass directly to the muscle without interruption, and the nerve cell from which the axons arise is situated within the central nervous system. Secondly, there are efferent nerve channels which,

instead of going directly to the organ to be supplied, terminate at a nerve cell located in a ganglion. Such fibres are called 'pre-ganglionic.' The nervous message is then transmitted through another nerve fibre, which is therefore post-ganglionic and innervates the organ or part concerned, in this case either a secreting gland, or involuntary unstriated muscle.

Examples of secreting glands which are thus innervated by post-ganglionic fibres are the salivary glands, the gastric and intestinal glands, the sweat glands and the lachrymal or tear glands. Examples of involuntary muscle innervated in the same kind of way are the muscles of the stomach and intestine, those of the uterus and bladder, as well as the muscles of the heart and blood vessels. All these muscles are uncontrolled by the will, and act in a purely automatic way.

The autonomic system which supplies involuntary muscle and secreting glands may be divided into cranial, thoracic and sacral nerves, according to the region of the central nervous system from which they take origin. The thoracic autonomic system is frequently designated the sympathetic nervous system owing to an idea which formerly prevailed regarding its nature. It has already been shown in previous chapters that many organs have two sources of autonomic nerve supply, the functions of which are different or even antagonistic. Thus the heart is excited to beat faster by stimulating the sympathetic supply, and slowed down by stimulating the vagus or cranial autonomic fibres, the vagus nerves having been described as the 'reins of the heart.' Similarly the arteries receive vaso-constrictor and vaso-dilator fibres which arise from different regions of the central nervous system, but the constrictor nerve fibres are always thoracic autonomic (i.e. sympathetic) in origin, and it is these fibres which are acted on so powerfully by adrenalin, which is the active substance of the secretion of the suprarenal body.

THE CENTRAL NERVOUS SYSTEM.

The body wall of the cranium and of the vertebral canal is lined internally by a fibrous membrane called the dura mater. The central nervous system throughout is lined by another membrane termed the pia mater which is very vascular. In between these membranes and loosely attached to them is a

third membrane called the arachnoid membrane. All these membranes are composed of connective tissue.

Both brain and spinal cord contain grey matter and white matter. The grey matter consists of nerve cells together with their smaller processes and a framework of supporting cells called neuroglia. The white matter consists entirely of nerve fibres

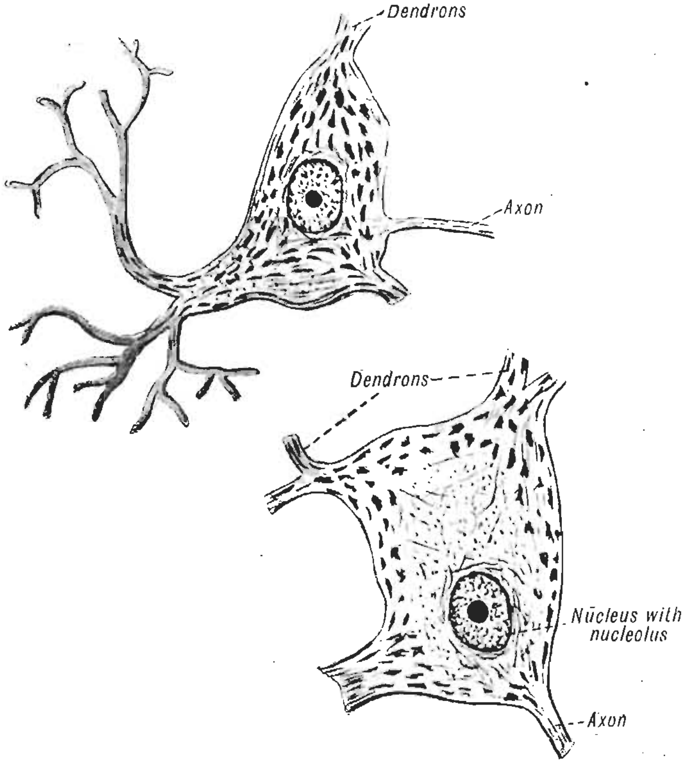


Fig. 46. Nerve cells from spinal cord of ox.

representing axons of cells in the grey matter and tending to run in parallel strands along the length of the cord. It is soft and pulpy and contains very little connective tissue.

The Brain. The different parts of the brain are described in every text-book on anatomy, and it will suffice here to give a very brief description of the principal of these parts with some reference to their more important functions.

The cerebrum which occupies a large part of the cranium is divided into the two hemispheres. The surfaces of these are convoluted, the extent of the convolutions varying considerably in different species of animals. The grey matter is external to the white matter. The cerebral hemispheres are especially well-developed in man, being the seat of the intelligence. An animal without the cerebrum is incapable of conscious sensation and can perform no voluntary movement. It can respond appropriately to every kind of stimulus from outside, but it cannot originate, and it cannot associate its sensations. It is quite devoid of all reasoning power. A frog deprived of its central hemispheres will swim to land if put into water but once it has reached a position of rest it will remain in that position until interfered with by any

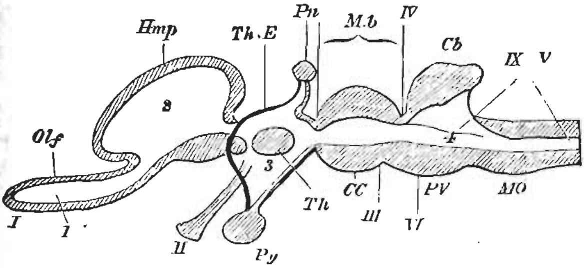


Fig. 47. Diagrammatic longitudinal section through brain (after Huxley, from Halliburton), *Olf.* olfactory lobe, *Hmp.* hemisphere, *Th.E.* thalamencephalon, *Pn* pineal body, *Py* pituitary body, *Th.* optic thalamus, *M.b.* mid-brain, *CC.* crura cerebri, *Cb.* cerebellum, *PV.* Pons Varolii, *MO.* medulla oblongata, *I—IX*, cranial nerves, 1—4, cavities or ventricles.

fresh stimulus. A dog so deprived will eat and perform all its essential bodily functions, but it will never recognise its master, nor carry out any act implying intelligence. The hemispheres contain certain areas associated with particular functions and any injury to these areas destroys or deleteriously affects the discharge of the function in question. Thus there is a visual and an auditory area, and areas for taste and smell, as well as for tactile and muscular sensibility, for speech, for the association of ideas, and various other functions.

The two hemispheres are connected by a transverse commissure called the corpus callosum. The hemispheres are connected with the medulla or hind brain by two large bands of nerve fibres called the crura cerebri. The olfactory lobes project forward from beneath the front end of the hemispheres.

The thalamencephalon is the vesicle of the fore brain fron which the *hemispheres* arise in development as hollow outgrowths It comes to be completely obscured by the hemispheres. Her all the afferent nerves of true sensation meet and then extend t the hemispheres.

The corpora quadrigemina or optic lobes are also almos completely covered by the hemispheres. They contain centre for the adjustment of the pupil of the eye for light, for sneezing and for various other movements.

The cerebellum lies behind the hemispheres. Its surface i

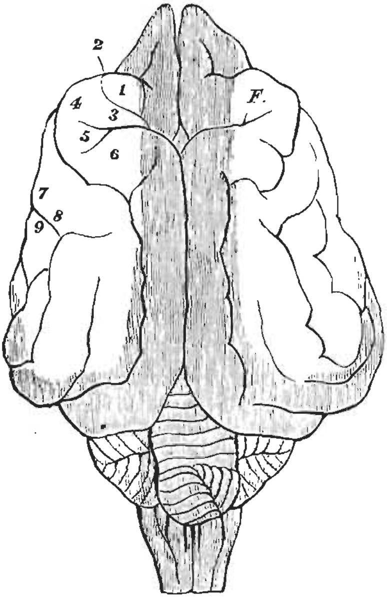


Fig. 48. Brain of dog (after Dalton, from Halliburton). F frontal fissure; 1—9 motor areas (1 and 2 for head, 3—6 limbs, 7—9 facial muscles).

folded, and it has grey matter outside and white matter withi It is in reality a paired expansion of the *pons*, just as the cerebru is a paired expansion of the extreme anterior end of the centra nervous system. The cerebellum receives afferent nerves fro the semi-circular canals of the ear, and from many joints, muscle and tendons concerned with bodily movement. Nerve fibre pass from this part of the brain to other parts of the centra nervous system and especially to the spinal cord. Injury to

the cerebellum is followed by lack of coordination in muscular movement.

The pons Varolii is a stout band of nerve fibres passing transversely across and in front of the medulla oblongata. It connects together the two sides of the cerebellum. It contains the centre for closing the eyelids in the presence of strong illumination.

The medulla oblongata or hind brain is a continuation of the spinal cord within the cranial cavity. It differs from the cord in having white matter penetrating the internal grey matter. In the medulla large strands of white fibres in passing back from the cerebral hemispheres cross over one another to the opposite side, and it is for this reason that injury (as in an apoplectic fit) affecting one side of the fore brain produces a condition of paralysis, not on the same side, but on the opposite side of the body. The medulla contains numerous centres presiding over particular functions, some of which have been referred to in previous chapters. Thus the centres regulating the respiratory movements, the beating of the heart, the secretion of saliva and gastric juice, and the movements of the oesophagus, stomach and intestines are situated in the medulla.

The cavities of the cerebral hemispheres are termed the lateral ventricles, that of the thalamencephalon is the third ventricle, and that of the medulla is the fourth ventricle.

The cranial nerves with their points of origin may here be enumerated, but for detailed accounts of their respective courses the reader is referred to text-books on anatomy. The nerves arise in pairs and are as follows:

1. Olfactory, or nerves of smell, arising from the front of each cerebral hemisphere.
2. Optic, or nerves of sight, arising from the thalamencephalon.
3. Ocular-motor innervating some of the muscles of the eyeball and arising from the region of the corpora quadrigemina.
4. Trochlear, motor nerves supplying the superior oblique muscle of the eyeball, and arising from the same region as the 3rd nerves.
5. Trigeminal, so-called because on each side they divide into three; they contain sensory fibres for the mouth and tongue, and motor fibres for the muscles used in mastication; they arise from the pons.
6. Abducens, motor nerves supplying the external rectus of the eyeball, and arising just behind the pons from the medulla.
7. Facial, motor nerves supplying the muscles of expression (in face, mouth and lips) and arising immediately behind the trigeminals.
8. Auditory, or nerves of hearing, arising from the sides of the medulla.

9. Glossopharyngeal, partly sensory and partly motor nerves, supplying the tongue and muscles of the pharynx, and arising from the side of the medulla.

10. Vagus, or pneumogastric, partly motor and partly sensory, passing from the sides of the medulla and running down the neck and thorax to the abdomen, and giving branches to the larynx, lungs, heart, oesophagus, stomach, intestines, and liver.

11. Spinal accessory, motor nerves, arising by ten rootlets from the medulla and spinal cord, and supplying certain muscles in the neck.

12. Hypoglossal, arising from the ventral surface of the medulla and supplying the muscles of the tongue.

The *spinal cord* is continuous with the medulla and passes backwards through the spinal canal inside the vertebral column as far as the lumbar region. Like the brain it is composed of both grey and white matter, but the grey matter in the cord is

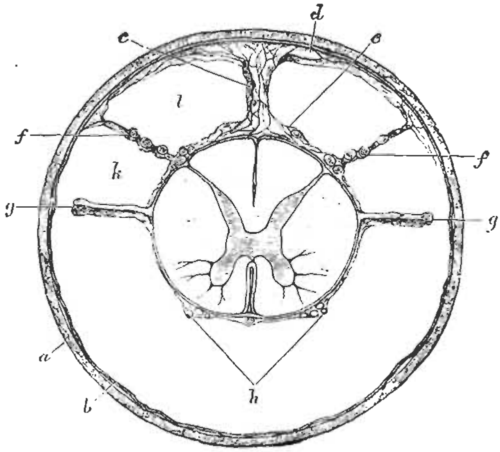


Fig. 49. Section through spinal cord within its membranes (after Key and Retzius, from Schafer). *f* bundles of posterior root, *h* bundles of anterior root, *a*—*g* membranes, trabeculae etc., *k*, *l* spaces.

always centrally placed and gives off symmetrically on each side a dorsal and a ventral horn, and in some regions a lateral horn. The dorsal and ventral horns are clearly shown in any transverse section through the cord. There is a deep dorsal fissure almost joining a shallower and more open ventral fissure, and these fissures divide the cord into two lateral halves excepting for the median portion between them in the middle of which is the central canal. The fissures are partly filled with connective tissue which contains vessels and passes into the substance of the cord supplying it with blood.

The white matter which lies on the outside of the grey matter ontains fibres connecting together the different parts of the entral nervous system. These fibres convey impulses up and own the cord, and one well-marked tract of white matter coming rom the cerebral hemispheres is believed to be concerned with he coordination of skilled movements.

The spinal nerves are given off in pairs at regular intervals rom the cord. Each nerve arises by two roots, one dorsal and ne ventral. The dorsal root contains only afferent fibres, and ach has its ganglion containing the nerve cells of the fibres. 'he ventral root contains efferent fibres. The two roots join ne another a short distance from the cord, and form a mixed erve trunk containing both sensory and motor fibres, the anglia of the dorsal roots being situated a short distance away rom the cord and near the place where the two sets of fibres nerge to form a single trunk containing mixed fibres. If the dorsal oot is destroyed, the sensations which the nerve fibres normally

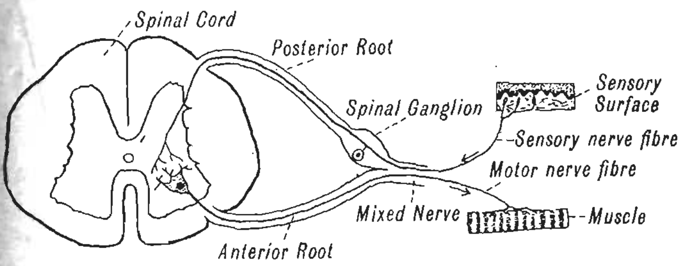


Fig. 50. The simple reflex arc.

onvey can no longer be felt. Similarly if the efferent fibres of he ventral root are destroyed, although the sensations conveyed y the fibres of the dorsal root are felt, the muscles in the part f the body concerned (e.g. those of an injured limb) are paralysed nd can no longer respond to stimuli by appropriate movements.

If the spinal cord is transected as by an animal breaking its ack the portion of the cord posterior to the break will be cut ff from the higher centres of the brain, and all those parts of the ody which are innervated from the isolated region of the cord 'ill be devoid of feeling. Nevertheless, reflex action can still ccur in those parts, since afferent impulses can enter the cord nd efferent impulses pass out although unaccompanied by ensation. Thus a frog whose brain has been destroyed, if its oot is pinched or irritated by an acid, will withdraw its leg or

attempt to rub away the source of irritation with its other leg, but it is incapable of sensation and unconscious of its actions.

As has been shown already the spinal cord contains numerous centres which preside over certain necessary functions of the body (e.g. defaecation, micturition, seminal ejaculation, penile erection, and parturition) and admit of the appropriate reflexes being carried out. But in the normal uninjured animal it is also the function of the cord to transmit sensory impulses to the higher centres of the brain, and so to bring the consequent motor impulses under the control of the volition.

Inhibition and Sleep. Certain efferent nerve fibres passing to glands or muscles are not excitatory but inhibitory in function, and if stimulated will prevent the continuance of the active process which otherwise would have gone on. Thus, according to Pawlow, the vagus contains fibres which are inhibitory for pancreatic secretion. The vagus also contains fibres which may be inhibitory to the heart's action, and can transmit impulses which produce increased resistance to transmission from auricle to ventricle. Moreover, certain parts of the brain can exert an inhibitory influence over centres situated posteriorly. Thus Sherrington found that after cutting through the crura cerebri centres for certain groups of muscles were greatly increased in excitability. The centres in question are situated between the crura cerebri and the medulla, and normally their activity is partially inhibited by the cerebral cortex.

Bayliss has suggested that sleep is a condition of inactivity (displayed by the parts of the brain associated with consciousness) which follows on inhibition if no further excitatory stimuli occur. The inhibition may be brought about by a stimulus as in the case of a child who is soothed to sleep by a lullaby. After all excitatory stimuli have been removed, the inhibition itself disappears and sleep continues as a zero state, excitation and inhibition both being absent. It is well known that hypnotic sleep in man is caused by stimuli from without, and these stimuli must be supposed to produce a state of inhibition in nerve centres in the brain.

The unconscious state characteristic of sleep can be brought to an end by excitatory stimuli of relatively great intensity. Taking advantage of this fact the deepness of sleep may be measured by the intensity of the stimuli which are necessary

to awaken the sleeper. Thus it has been ascertained in man that sleep is most intense during the first hour and a half (after the first few minutes) and then becomes rapidly less. Thus sounds which fail to wake the sleeper during the early hours of the night, will bring sleep to an end at any time from the beginning of the third hour onwards.

Apart from loss of consciousness, certain other physiological phenomena characterise sleep. The respirations and the heart beats become slower. Secretory activity, such as that of the kidney, or of the mucous glands is diminished. It is believed however that the digestive organs are little if at all less active during sleep, provided that there is food in the stomach or intestines. The supply of blood to the brain is said to be diminished during sleep, and this according to some is one of the main factors inducing sleep. On the other hand, according to Howell, the diminished supply of blood is of the nature of a result, the cause being fatigue on the part of the vaso-motor centre in the medulla. As a result of constant activity in the daytime this centre is supposed to become so fatigued that it is no longer able to maintain a sufficient flow of blood through the brain, and unconsciousness or sleep is the result.

Sleep is the period of rest and recuperation when the constructive or anabolic side of animal activity dominates over the destructive or katabolic side. Want of sleep is even more damaging than starvation, for dogs deprived of food for three weeks may yet undergo recovery, whereas after five days without sleep they die. But why the state of sleep should recur normally with such rhythmical regularity and what are the precise factors in metabolism which govern this recurrence, are questions which on the evidence available admit only of very imperfect solutions. That night is the time for sleep, both with man and with most animals, is known to all, and it is obvious that the setting in of darkness is its immediate cause, while the daylight which comes at dawn is the stimulus for awakening.

CHAPTER IX

THE ORGANS OF SPECIAL SENSE[1]

The organs of special sense have been alluded to in the preceding chapter. It will suffice here to give a short description of the eye, the ear, and the organs of taste and smell.

The Eye. The eye is an organ specially adapted to receive and retain visual impressions. It is a globular structure, consisting for the greater part of a tough white fibrous coat, the

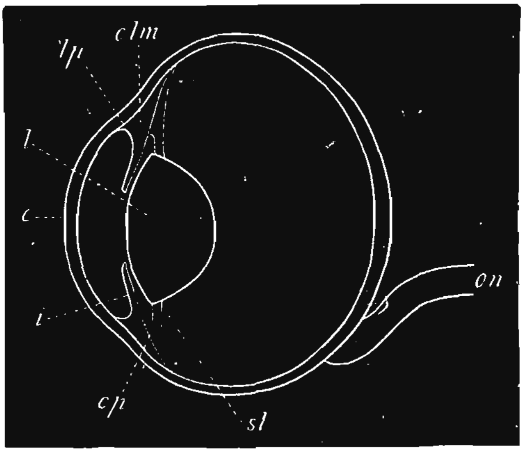


Fig. 51. Vertical section of the eye of the horse, natural size. *c*, cornea; *l*, lens; *i*, iris; *cp*, ciliary process; *lp*, ligamentum pectinatum; *clm*, position of ciliary muscle; *sl*, suspensory ligament of lens; *on*, optic nerve, showing its curve. Note its attachment to the lower part of the globe. (From Smith, Messrs Baillière, Tindall and Cox.)

sclerotic coat, bounded in front by a transparent watch-glass-like structure called the *cornea*. Inserted into the sclerotic coat towards the front portion of the eyeball are six muscles, the superior and inferior oblique muscles, the superior and inferior rectus muscles, and the internal and external rectus muscles. These muscles, which all find their origin in the rear of the bony orbit

[1] By Capt. E. T. Halnan, M.A.

or eye socket, by their action control and facilitate the movement of the eyeball in any desired direction. Together they play an extremely important part in the case of man in ensuring that the images received by the two eyes give rise to a single visual impression.

The accessory structures, the eyelids, eyelashes, and the lachrymal glands, together with the conjunctiva, a delicate membrane lining the inner surface of the eyelids and continued over the front surface of the eyeball, protect the eye from the liability to injury from dust and other foreign bodies. The watery secretion from the lachrymal glands continually floods across the surface of the conjunctiva to the inner angle of the eyes, whence it drains away through the lachrymal duct to the nasal cavity, carrying with it any dust particles which may have lodged on the surface of the conjunctiva.

The internal structure of the eye. A longitudinal section through the eyeball demonstrates that the eye is divided into two compartments by a delicate, elastic, transparent, lenticular-shaped body, the crystalline lens, which is doubly convex, and is held in place by a strong membranous frame called the suspensory ligament, which in turn is itself inserted into the inner or choroid coat of the eyeball. The front compartment, bounded externally by the cornea and internally by the crystalline lens, is filled with a semi-fluid, transparent substance called the aqueous humour. The posterior compartment is also filled with a clear jelly-like substance called the vitreous humour, and these humours by their action cause the eye to preserve its globular shape. Lying in front of the crystalline lens is a pigmented, curtain-like structure called the iris which is pierced in the centre by an aperture, the *pupil*, through which the light rays penetrate into the interior of the eye. The shape of the pupil varies in the domestic animals, in man and the dog it is circular, in the horse, sheep and ox it is elliptical, the long axis of the ellipse being horizontal. The iris itself is pigmented, is opaque to light, contains circular and longitudinal unstriated muscular fibres, which by their action cause the pupil to *dilate or contract* and thus regulate the amount of light which is allowed to pass through the crystalline lens.

Action of the crystalline lens. Light rays passing from a near or distant object and falling on the surface of the eye are refracted or bent in passing through the crystalline lens and are brought to

a focus on the hinder part of the inner surface of the eye, so forming an inverted image of the object in a way similar to that in which the lens of a camera, when properly focussed, throws an image on the ground glass focussing screen. By the contraction or relaxation of a muscle, called the ciliary muscle, the crystalline lens is made more or less convex and a sharp image of the object looked at is thrown on the back interior surface of the eyeball. Inability to focus the image sharply gives rise to the defects of vision known as longsightedness (presbyopia) and shortsightedness (myopia). Stretching over the posterior two-thirds of the inner surface of the eyeball is a delicate nervous curtain, the *retina*, and

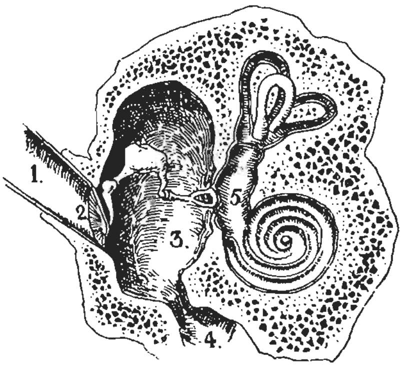


Fig. 52. Diagrammatic section of the horse's ear. 1, External auditory canal; 2, the tympanum; 3, chain of bones across the middle ear; 4, the Eustachian tube; 5, the internal ear; the number is on the vestibule, above which may be seen the semi-circular canals, while below is the cochlea. (From Smith, Messrs Baillière, Tindall and Cox.)

it is on this curtain that the image is thrown and focussed. The retina, which is partially formed from the continuation of the fibres of the *optic* nerve, is a very complex structure and contains the sense end-organs, the stimulation of which by the action of light give rise to the sense of perception in the brain.

The Ear. The auditory apparatus consists of three parts—the external ear, the middle ear, and the internal ear. The internal ear contains the essential mechanism which converts the external waves of sound into a condition suitable for transmission into the brain, the middle and external ear acting as agents for the collection and transmission of sound to the internal ear.

The *external ear* is made up of the pinna and the external auditory meatus. The pinna, which is varied in shape, is composed chiefly of elastic fibro-cartilage, invested with a thin closely adherent skin. In the domestic animals muscles are present which enable the animal to move the pinnae in the direction of the source of sound. The pinnae by their shape serve to collect and intensify the sound waves transmitted through the air in the direction of the animal. From the central hollow or concha of the pinna passes a canal, the external auditory meatus, along which the sound waves pass. The external auditory meatus consists partly of cartilage and partly of bone and at its termination in the bony part of the skull is bounded by a parchment-like membrane called the tympanic membrane, or drum of the ear.

The *middle ear* consists essentially of a cavity in the temporal bone of the skull, is lined for the most part with ciliated mucous membrane, and communicates with the cavity of the mouth by means of the cylindriform canal called the Eustachian tube, the external opening of which occurs in the pharynx. The function of the Eustachian tube is to allow the passage of air from the exterior to the middle ear, thus allowing for variations of pressure of the atmosphere and ensuring equality of pressure on both sides of the tympanic membrane.

The walls of the middle ear are bony except where interrupted by small apertures covered with membrane, as at the fenestra rotunda and fenestra ovalis, and in the outer part, the tympanic membrane. The tympanic membrane is tightly stretched in an oblique direction across the end of the external auditory meatus, forming a division between this canal and the middle ear. Stretching from the tympanic membrane across the cavity of the middle ear to the fenestra ovalis is a chain of three small bones, the auditory ossicles, called by reason of their shapes the malleus, incus and stapes. The malleus is attached to the tympanic membrane and the foot of the stapes (or stirrup bone) is attached to the fenestra ovalis, the incus articulating between these two bones.

The tympanic membrane and the fenestra ovalis are also provided with small but relatively strong muscles which by their action vary the tension of these two membranes as required.

The *internal* ear, or ear proper, consists of a membranous bag (the membranous labyrinth) filled with a fluid called the endolymph, and this bag is lodged in cavities of the petrosal portion

of the temporal bone specially hollowed to receive it. Between the membranous labyrinth and the investing bony or osseous labyrinth is a fluid called the perilymph.

The osseous labyrinth consists of three portions, the vestibule, the cochlea and the semicircular canals (see p. 96). The vestibule, or middle cavity, presents several apertures through which penetrate divisions of the auditory nerve. The portion of the membranous bag or labyrinth lying within the vestibule forms two communicating compartments, the utricle and the saccule. Into the utricle open the semicircular canals, while the saccule communicates with the canal of the cochlea by a small canal called the canalis reuniens. The cochlear portion of the osseous labyrinth resembles in shape a snailshell, the circular coil consisting of two and a half turns, closed at its upper termination, but presenting openings at the base for the fenestra ovalis, the fenestra rotunda and the canalis reuniens. A section through one of the coils reveals the fact that the coil is separated into three portions, the scala media or canal of the cochlea, the scala vestibuli and the scala tympani. The division of the cochlea into the scala vestibuli and scala tympani is effected by a flat sill-like projection of bone from the internal surface of the coil (the lamina spiralis), the outer edge of this spiral being continued to the outer border of the coil by a membrane called the basilar membrane. On this membrane rests the canal of the cochlea. The scala vestibuli is closed at its basal portion by the *fenestra ovalis* and communicates with the scala tympani at its apical end by a small aperture called the *helicotrema*. The scala tympani in its turn is closed at its basal portion by the fenestra rotunda.

Nerve distribution. The auditory nerve divides into two branches, one of which supplies the utricle, saccule, and the semicircular canals, the other or cochlear branch, running up the centre of the cochlea, giving off branches through the lamina spiralis, these branches terminating in fine filaments which form special end sense organs in the canal of the cochlea. These sense end organs have a complicated structure and are known collectively as the organ of Corti.

Physiology of hearing. The transmission of sound waves to the brain takes the following course. The wave-like concussions caused by the vibration of air particles against the tympanic membrane causes this tightly stretched membrane to vibrate

rapidly. These vibrations are communicated to the bony ossicles, which undergo varied movements. The stapes, which as we have already seen, is attached to the fenestra ovalis, causes this membrane to vibrate and so sets up a series of vibratory waves in the perilymph which fills the scala vestibuli. These waves travel up the cochlea, pass through the helicotrema, travel down the scala tympani and end against the fenestra rotunda which in turn is set in vibration. During their passage through the cochlea these vibration waves impinge on the membranes enclosing the canal of the cochlea setting up a sympathetic series of vibrations in the endolymph of the canal of the cochlea and so act on the delicate nerve endings in the organ of Corti. The stimuli thus received are conveyed to the brain and give rise to the sensation of hearing.

The Sense of Taste. The sense of taste is associated with the presence of certain well defined groups of cells, called gustatory cells, which are found in the characteristic papillae of the mucous membrane of the tongue and are restricted to well-defined areas. According to their shape, these papillae or projections are called filiform, fungiform and circumvallate papillae, and the fungiform and circumvallate papillae are specially associated with the sense of taste. The gustatory cells are found in bud-like groups and are called taste buds. In the ox, the fungiform papillae are numerous and distinct and are found scattered over the dorsum and edges of the free part of the tongue. The circumvallate papillae number 8 to 17 on each side and each side forming a narrow group at the edge of the base of the tongue. In the horse the fungiform papillae are large and easily seen and occur principally on the lateral part of the tongue. The circumvallate papillae are two or three in number, the two constant ones being ½ in. or more in diameter and are found on the upper surface of the base of the tongue, one on each side of the middle line about an inch apart. Foliate or leaf-like papillae are also present on the anterior pillars of the soft palate and contain taste buds.

Each gustatory cell is long and very thin, has a large nucleus at its middle point, and ends in a delicate process which projects like a stiff hair through the open mouth of the taste bud. The papillae are supplied with branches from two nerves, the glosso-pharyngeal nerve, and the gustatory nerve which is a branch of the 5th cranial nerve. There is evidence for the belief that different taste sensations are supplied by these two nerves. In the case of

man, we find that tastes may be classified under four chief heads: sweet, bitter, sour or acid, and salt. In order to taste a substance it must first be dissolved, in order to act upon the gustatory cells.

The Sense of Smell. The sense of smell is very well developed in animals and plays a large part in their normal life and habits. The organ of smell consists of a well-defined area of mucous membrane lining part of the nasal cavities, and characterised by the absence of cilia. This olfactory region, as it is called, is well supplied with branches of the olfactory nerve, together with a few fibres from the 5th cranial nerve. The olfactory mucous membrane contains cells of two kinds, those associated with the production of the sense of smell, numerous, long slender rod-shaped cells, and others whose chief function is to support the true olfactory cells with which they are intermixed. The sensation of smell arises through the stimulus of minute quantities of odoriferous matter exciting the olfactory cells, the stimulus thus created being carried back through the olfactory nerve to the brain.

CHAPTER X

THE ORGANS OF LOCOMOTION

The muscular tissues of an animal have the special function of altering the positions of various parts of the body relative to one another. By means of this function, which is due to the contractility of the tissue and its capacity to respond to nervous impulses, locomotion is effected. The principal kinds of muscle have been already sufficiently described. It has also been mentioned that whereas the muscles of the heart and blood vessels and the unstriated muscles generally are involuntary, those of the limbs, which are striated, are under the control of the will.

The contraction of a particular muscle (e.g. the gastrocnemius of the calf of the frog's leg) can be caused experimentally by stimulating electrically the nerve which supplies it (e.g. the sciatic), and if the stimuli are made to succeed one another at a rate such that the muscle has not begun to relax before the next stimulus reaches it, it is driven into a condition of continuous contraction or 'tetanus.'

The process of contraction in muscle is associated with the splitting off of lactic acid, but at first there is no evolution of carbon dioxide. This takes place in the second stage which succeeds the contraction stage. Fats or carbohydrates are then oxidised, and the lactic acid is restored to the muscle. Energy is set free equivalent to the heat evolved and the work done, the former being utilised to keep up the temperature of the body.

It is well known that exercise increases muscular efficiency. This is due partly to the direct effect of exercise in developing the muscles, and partly to the fact that with repeated usage the muscles work more economically, those which are superfluous remaining at rest. It is only after repeated trials that the nervous impulses become properly distributed to the necessary muscles.

The composition of muscular tissue varies within considerable limits owing to the inconstant quantities of fat or connective

tissue present. The following represents the approximate average composition after removal of the more obvious fat:

Protein	18	per cent.
Fat and gelatin	4	,,
Glycogen, etc.	·9	,,
Salts	2·1	,,
Water	75	,,

The muscles of motion and locomotion act in virtue of their property of contraction. They are attached to bones by tendons, one tendon being attached to one bone and the other tendon to a separate bone, the muscular fibres in between passing over one or more joints. The attachment to the more stationary bone is usually referred to as the origin of the muscle, while the attachment to the more movable bone is generally called the insertion. Muscles can contract to about two-thirds of their normal length.

We may now consider very briefly some of the chief muscles in the fore and hind limbs of the horse, and then pass on to the mechanical laws under which these muscles work.

The Muscles of the Fore limb. The shoulder blade is connected to the trunk by a very strong muscle (the serratus magnus) which is attached to the last five cervical vertebrae, to the first eight ribs and, in the middle, to the inside of the shoulder blade. When the front portion of the muscle contracts, the shoulder is drawn forwards. When the rear contracts it is drawn backwards.

The upper part of the shoulder blade is connected to the trunk by a muscle attached to the inner extremity of the former, and having one branch (the dorsal trapezius) going to the withers and the other (the cervical trapezius) going to the suspensory ligament of the neck. When the latter branch contracts it draws the shoulder blade forwards. When the dorsal trapezius contracts it has the reverse effect.

The fore limb is drawn forwards chiefly however by a muscle attached at one end to the head and top of the neck and at the other end to the middle of the humerus. The fore limb is drawn backwards by the action of two muscles. The first of these is attached to the sternum at one end, and to the humerus and shoulder blade at the other. It pulls the limb backwards and downwards. The second muscle is attached to the dorsal and lumbar vertebrae and to the humerus. It pulls the limb backwards and upwards.

When the fore limb is advanced, the shoulder blade is extended

nd the elbow flexed. This action is due to the contraction of muscle (the flexor brachii) attached at one end to the front of he shoulder blade and at the other end to the front of the radius ust below the elbow joint.

The chief muscle that extends the 'knee' or wrist (the extensor etacarpi magnus) has its origin in the front part of the humerus; t runs down the fore-arm, its tendon passing over the 'knee' and eing inserted on the head of the cannon bone.

The three muscles that bend the knee take origin on the back f the humerus just above the elbow and are inserted on the plint bones (internus, medius and externus metacarpi flexor).

The two muscles which extend the fetlock, pastern and coffin oints run down the front of the fore-arm. One has its origin n the head of the radius and is inserted on the front of the large astern bone (extensor metacarpi). The other starts on the umerus above the elbow and passes to the front part of the offin bone (extensor pedis).

The muscles that flex the fetlock, pastern, and coffin joints, nd also aid in bending the knee, take their origin just above the lbow joint at the back of the humerus, and proceed down the osterior side of the fore-arm. A little above the 'knee' they ecome joined to their tendons. These are attached one to the ase of the coffin bone (the flexor pedis perforans tendon), and he other to the small pastern or coronet (the flexor pedis perforatus tendon).

The Muscles of the Hind limb. The hip is extended by the roup (gluteal) muscles, and also by some muscles which lie at he back of the femur. It is flexed by muscles which have their rigin on the under surface of the lumbar vertebrae and are nserted on to the femur.

The stifle (true knee) is extended by a muscle (triceps extensor) which has its origin on the under surface of the pelvis oint in front of the hip joint, and is inserted on the patella or nee cap. It is flexed by a muscle attached to the portion of the elvis behind the hip joint, and to the tibia.

The hock is extended by the gastrocnemius which has its rigin on the lower end of the femur, and is inserted by tendons n the point of the hock. One of the tendons (the one passing nderneath) terminates at the hock, but the other (the flexor edis perforatus) passes to the small pastern, and is the flexor of

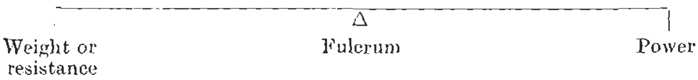
the fetlock. Thus the hock cannot be extended without the fetlock being flexed. The flexor metatarsi bends the hock

The joints below the hock are extended by muscles which take origin near the stifle, run down the front of the limb, are continued as tendons down the front part of the cannon bone, and finally are inserted on the pastern and coffin bones. They are flexed by a muscle originating at the back of the upper portion of the tibia behind which it runs down to the hock joint where it is continued as a tendon (flexor perforans), and terminates, as in the fore limb, at the bottom of the coffin bone.

The Mechanics of Locomotion. The principal kinds of movements which the limbs may be made to undergo by the contraction and expansion of their muscles may be classified naturally under four heads: (1) Flexion or bending, (2) Extension or straightening out, (3) Abduction or drawing away from the middle line, and (4) Adduction or bringing to the middle line. To these may be added (5) Rotation, when a limb is made to turn on its own axis, and (6) Circumduction, when it is made to describe a conical surface by rotation around an imaginary axis.

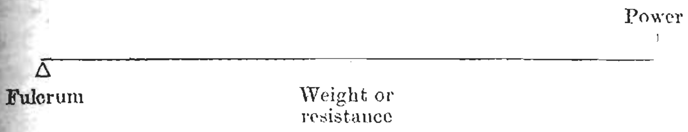
Now in a large number of these movements a joint is involved, and the bone of the part which moves acts as a lever, and turns about that portion of itself which forms part of the joint concerned and acts as a relatively fixed point or fulcrum. We may now consider the three kinds of levers, and then proceed to give examples of these levers as shown by the movements of certain of the limb muscles which have been already described.

In the first kind of lever the fulcrum is between the weight and the power. It is the lever of power and in the body it is the lever of extension. Thus in extending the hind leg, the centre of the hock joint is the fulcrum, the gastrocnemius is the power the distance from the summit of the calcaneum to the centre of the hock joint is the power arm, the leg below the hock is the weight and the length of the metatarsus is the weight arm.

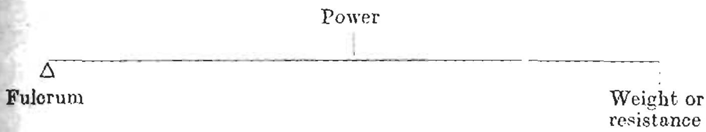


In the second kind of lever the fulcrum is at one end and is nearer to the weight than to the power. This lever is not common

in the body. It occurs when the leg is fixed on the ground and the body is passing over it. The ground is the fulcrum, the gastrocnemius is the power, and the body through the elbow or hock joints is the weight.



In the third kind of lever the fulcrum is at one end but is nearer to the power than to the weight.

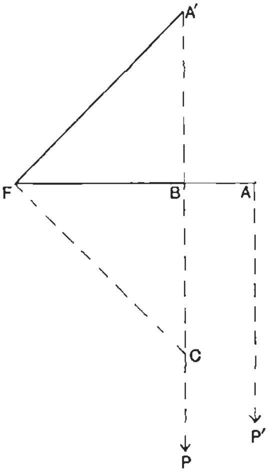


In the body it is the lever of flexion, and the nearer the power to the fulcrum the greater is the degree of flexion obtained for the same expenditure of muscular force. It is the lever of speed and what is gained in speed is lost in power. In one sense therefore it is a wasteful lever. In the horse it is commoner than the other two levers, since in that animal the movements of the limbs are directed principally towards carrying a comparatively light weight a considerable distance and in a short time. The following are examples. In the flexion of the elbow the weight is the leg below the elbow, the power is the flexor brachii muscle (which is inserted on the radius) and the fulcrum is the elbow joint. In the flexion of the hock the weight is the limb below the hock, the power is the flexor metatarsi, and the fulcrum is the hock joint.

In the three classes of lever as drawn above the power and weight are represented as working at right angles to the lever. In the actual levers of the body this is not the case. But the nearer the force is to being at right angles to the lever the greater is the mechanical advantage.

Thus if AP in the diagram represents the line of action of the force exerted by a muscle attached to a bone FA at A and causing by its contraction movement of the bone round the joint at F, the mechanical advantage may be represented by $P \times FA$ where FA is at right angles to the line of action of P.

If however the bone is not at right angles to AP but is, say, in the position FA' or FC the mechanical advantage is not measured by



$$P' \; (=P) \times FA' \text{ or } P' \times FC$$

but by $P' \times FB$ where FB is at right angles to the line of action of P' or P. FB is greatest when it is equal to FA, that is the mechanical advantage is greatest when the force exerted by the muscular contraction acting at its attachment is at right angles to the bone. Acting on this principle the cart horse, with a view to obtaining the utmost mechanical advantage when drawing a load, will endeavour to move the levers of its limbs in such a way that the power is in each case as nearly as possible at right angles to the lever. Thus the best results will be obtained by only slightly bending the joints and consequently taking short steps. On the other hand a horse when galloping will require the power of straightening out its limbs to their utmost capacity, and thus will obtain speed at a lavish expenditure of muscular exertion.

It was formerly believed that the muscular attachment of the fore limb to the trunk showed that the body was simply slung between the fore legs which acted as props while the hind legs did the work. Photography however has shown that this view is quite erroneous, and that the fore legs as well as the hind act as propellers to the body. This is especially well shown in photographs of horses galloping when the fore leg may propel the animal 10 feet forward, and in so doing raise it four inches vertically from the ground.

Joints. Where two bones with moving surfaces come in contact joints occur. There are three chief kinds of joints: (1) ball and socket joints (as in the hip), (2) hinge-like joints (as in the hock), and (3) sliding joints (as in the knee). All these are covered with cartilage which is much more yielding than bone. The cartilage is covered by the synovial membranes which secrete the synovia or 'joint-oil.' This lubricates the joints and so

We may now consider the joints in the horse's limbs, beginning with the hind leg.

The Hock Joint. The principal movement of the hock takes place between the tibia and astragalus (a tarsal bone). Here the movement is simple and its range is great, but it is only in galloping and jumping that the angle formed by the tibia and cannon bone is much reduced. The movement between the tarsal bones is small and limited. It is in places of the nature of a rotation, as is shown by the presence of grooves on certain of the bones. The greatest amount of pressure comes on the anterior or inner surface of the bones, and it is here that we get the greatest damage in disease. The pressure is removed by flexing the hock which thereby rests the leg. Thus horses kept standing for a considerable time do not usually rest for long on both hind legs equally, but bend the hock of first one leg and then the other in order to escape the effects of the continuously exerted pressure.

The Stifle Joint. This is the largest joint in the horse's body, and it has considerable scope for movement. Owing to the presence of oblique (instead of vertical) ridges on the astragalus a rotation or screw action is produced, not on the hock, but on the stifle. This is turned outwards during flexion of the leg so that it moves clear of the abdominal wall. When the foot is at rest and on the ground the muscles of the stifle (i.e. those passing from the femur to the patella) contract, and thus the leg is maintained in a state of rigidity.

The Hip Joint. This is a ball and socket joint. Its range of outward movement in the horse is restricted by ligaments inserted, not into the middle, but into the head of the femur, and on the inner side. This arrangement makes it difficult for a horse to 'cow-kick.'

The Shoulder Joint. The humerus has a great range of movement against the scapula, and thus the joint has very free play.

The Elbow Joint. The articulating surface is provided with ridges which help to keep the knees in position.

The Knee (or Wrist) Joint. Here there are three main joints and several lesser ones. The upper of these joints possesses great scope for movements; the lowest one is much restricted. The 'brushing' of the legs together in faulty movement is apparently due partly to the imperfect shape of the articular surfaces between

the radius and the proximal row of carpals in horses which are so affected.

The Fetlock Joint. Here we have a yielding articulation due to the two sesamoid bones. These bones help to bear the animal's weight in a state of rest, and provide an anti-concussion mechanism, saving the limb from jar when it comes to the ground.

Postures and Movements of the Horse.

When a horse is at rest the centre of gravity is stable; when it is in motion the centre oscillates backwards and forwards. If we draw a vertical line passing through a point six inches behind the shoulder and a horizontal line passing a little below the shoulder, the centre of gravity is approximately where these lines intersect. Thus the centre is nearer to the elbow than to the stifle. When pulling a load the centre is in front of the point in question; when backing a load it is behind it. In jumping the centre is behind this point when the hind legs leave the ground; it moves forward as the fore legs come to the ground. And similarly with the other motions.

It follows from the normal position of the centre of gravity that the fore legs bear a greater proportion of the total weight of the body than the hind legs, and it has been calculated that when carrying a rider, the fore legs bear two-thirds of the rider's weight and the hind legs one-third. It has been shown also that the amount of weight carried by the fore and hind legs respectively varies with the position of the horse's head. If the head is held well up, the fore legs carry less of its weight than if the head is drooping. It is important therefore to keep a stumbling horse in hand, and not to give him his head too much.

Standing. As already described the fore legs are connected with the body by the great serratus muscles. The hind legs have no such muscular attachments, but simple ball and socket joints. The horse is enabled to rest in a standing position, and thus to sleep while standing by the help of the suspensory and check ligaments. The suspensory ligament arises by two heads from the carpus and upper part of the cannon bone; it divides into two, a branch being attached to each sesamoid bone and continued downwards and forwards, finally joining the extensor tendon. Its function is to support the fetlock. Further, in order that the muscles attached to the humerus may be relieved of

strain, both their flexor and their extensor tendons are provided with ligamentous branches to the radius, carpus, and metacarpals. These are the check ligaments. In the hind limb we meet with the same sort of arrangement. As already remarked, a horse while standing does not normally keep its hind legs together, but flexes each one of them alternately so as to relieve the strain. On the other hand a horse almost invariably keeps its fore feet together while standing.

Lying Down. A horse in coming to lie down brings all its legs under its body; it bends its knees and hocks, the former together with its chest coming into contact with the ground before the hindquarters. When actually lying down a horse either rests on one side of its chest with two legs (a fore and a hind) underneath and the other two outside his body, or else it lies on its side stretched out. A cow can rest vertically on the ventral ridge of the sternum, but this attitude is impossible in a horse owing to the sharpness of the edge of that bone.

Rising. A horse in getting up off the ground stretches out both its fore feet in front, pressing upwards its hindquarters by fixing its hoofs firmly on the ground. The fore part of the body is the first to rise, not as in the cow or sheep where the hindquarters rise first.

Rearing. In rearing a horse brings its hind legs some distance under its body, and at the same time throws up its head, and all the legs are then used to raise the body upwards. A great strain is thrown upon the hocks, and the ligaments of this joint may become injured and curbs[1] induced.

Kicking. When a horse kicks the head is lowered and the croup is raised, and the hind legs are thrust suddenly and forcibly backwards. In 'cow-kicking,' which is fortunately unusual in horses, one hind leg is brought rapidly forward, after the manner of kicking in cattle.

Walking. There are four stages:

(1) The body is balanced on 3 legs.
(2) ,, ,, ,, 2 diagonal legs.
(3) ,, ,, ,, 3 legs.
(4) ,, ,, ,, 2 lateral legs (1 fore and 1 hind).

[1] Curb is the name given to the swelling on the straight ligament of the hock. It may result from any kind of strain on the hock, and is very common in cab-horses or any horses which are much used for driving on hard paved streets.

The next position is like the first only that the three legs employed are different. Considering the four movements more closely, we find:

in (1) the horse puts one fore leg (e.g. the off fore) forward;

in (2) the near hind leg is lifted, the horse standing on the near fore and off hind (i.e. on diagonal legs):

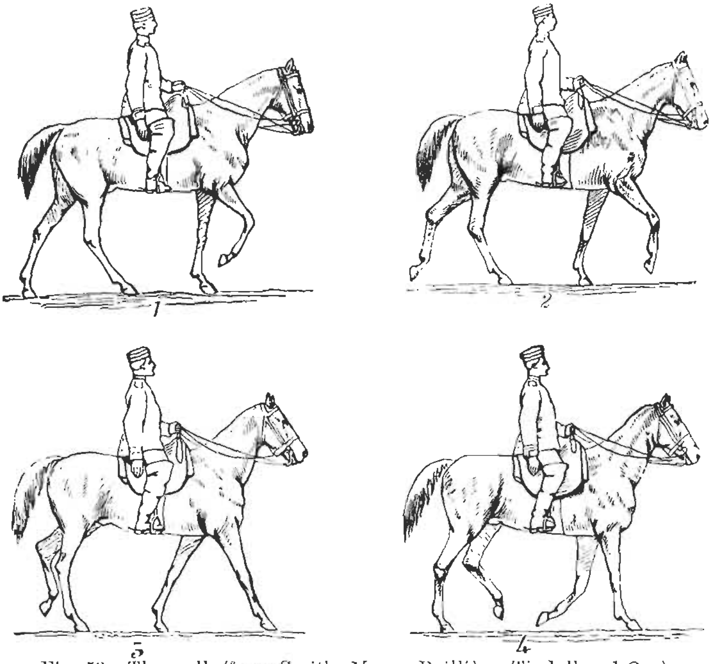


Fig. 53. The walk (from Smith, Messrs Baillière, Tindall and Cox).

in (3) the horse is balanced on both fore and the off hind leg;

in (4) the near fore and near hind are both put forward, the latter being advanced over the track of the near fore.

If a leg is not properly straightened by the extensor muscles the toe of the hoof comes to the ground first, and the horse stumbles.

Trotting. There are three stages:

(1) The body is balanced on two diagonal legs.

(2) All the legs are off the ground.

(3) The body is balanced on the other two diagonal legs.

The animal is propelled off the ground by the two pairs of diagonal legs (one fore and one hind) acting alternately.

If a horse falls while trotting, this is due to its knee not being properly flexed before extending its leg, or else it is due to the

imperfect extension of the leg which is thereby insufficient to carry the weight.

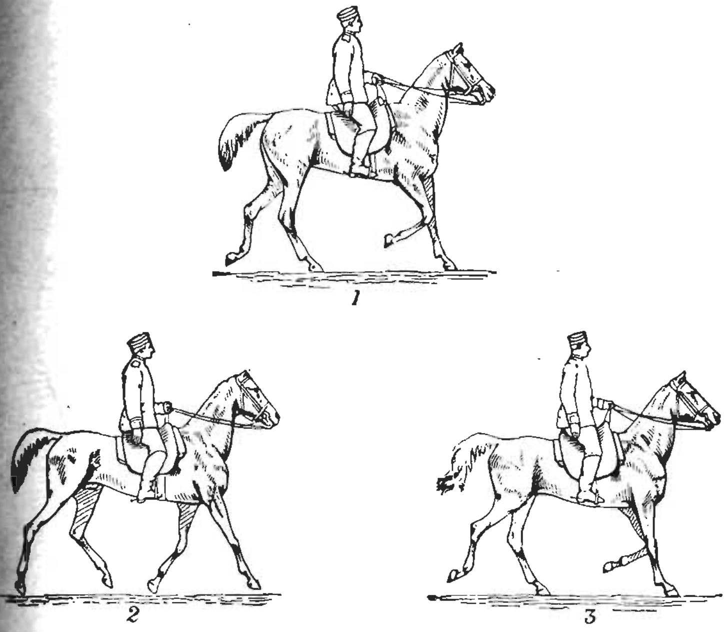


Fig. 54. The trot (from Smith, Messrs Baillière, Tindall and Cox).

Ambling. Lateral (and not diagonal) legs are on or off the ground at the same time (e.g. the off fore and off hind legs are lifted simultaneously, and not the off fore and near hind as in the trot). The amble is a very comfortable motion for the rider.

The Canter. There are six stages:

(1) The body is propelled upward and forward by one fore leg (e.g. by the off fore, the other three legs being off the ground).

(2) All the legs are off but near the ground.

(3) The near hind leg is on the ground.

(4) The off hind and near fore legs come to the ground, so that three legs (both hind and near fore) are on the ground.

(5) The off fore leg touches the ground, and simultaneously the near hind leaves the ground, so that three legs (now, both fore and the off hind) are on the ground.

(6) The near fore and off hind legs leave the ground, the horse being balanced on the off fore leg only.

The leading leg (in the case just described, the off fore) gives the body its final propulsion, and this causes it to become fatigued sooner than the others.

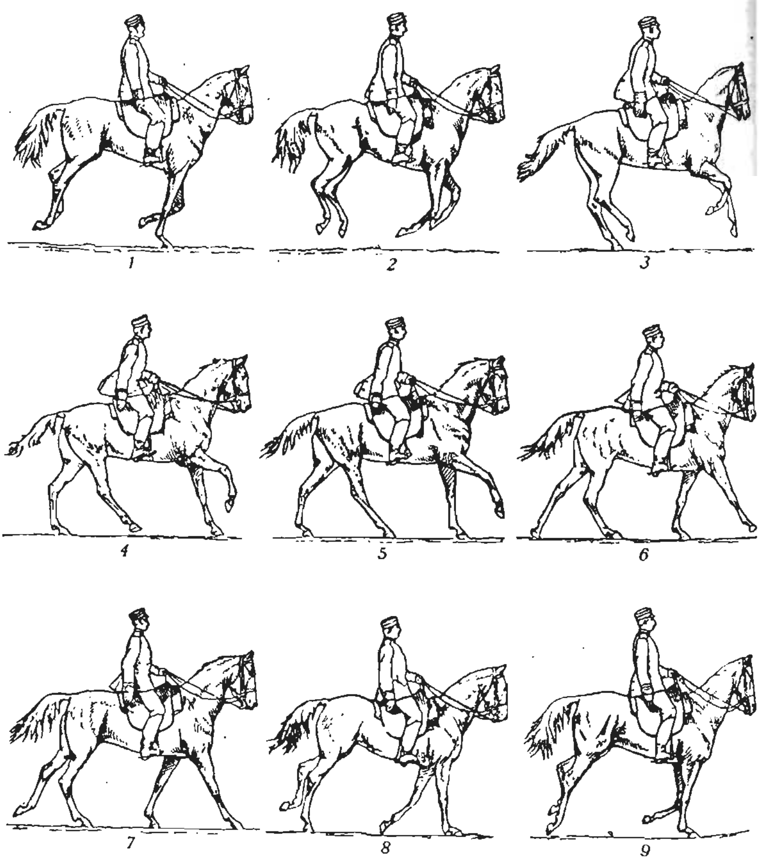


Fig. 55. The canter (from Smith, Messrs Baillière, Tindall and Cox).

The Gallop. This occurs in seven stages:

(1) The horse is in the air.

(2) One hind leg (e.g. the off hind) comes to the ground near the centre of gravity.

(3) The near hind leg comes to the ground (so that there are two legs in contact with the ground).

(4) The off fore leg comes to the ground, and the off hind is extended simultaneously.

(5) The near hind leg leaves the ground, the horse being balanced on the off fore leg only.

(6) The near fore leg comes to the ground, and the off fore leg leaves it, the body being balanced on the near fore leg only.

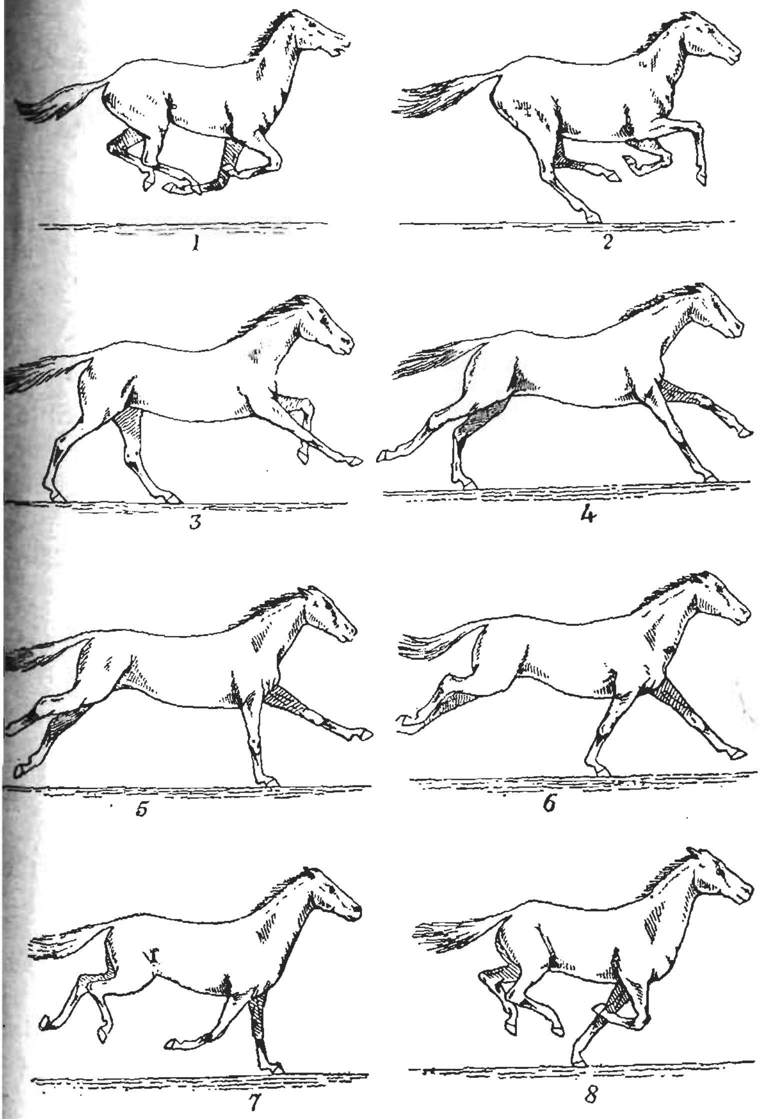


Fig. 56. The gallop (from Smith, Messrs Baillière, Tindall and Cox).

(7) The body passes over the near fore leg, and is then lifted off the ground as in the first stage.

The fore leg in propulsion rotates over the foot, the limb being extended in a straight line from the elbow to the ground. In the case of the hind leg propulsion is obtained partly by the foot being placed on the ground against which it presses, and partly by the straightening of the hock. It is estimated that the hock performs twice the work done by the knee, and this, as will be seen again later, is one of the reasons why the hock is more liable to injury than the knee.

The Horse's Foot.

The wall of the 'foot' or hoof is composed essentially and developmentally of two layers, (1) the horny part representing modified epidermis, and (2) the internal vascular part representing the dermis.

The front part of the foot is called the toe; the hind part the heel; between are the two quarters.

The wall is the part of the hoof which is visible when the foot is resting on the ground. The sole is the part which is in contact with the ground. The foot-pad or 'frog' is the pyramidal-shaped part of the hoof filling the space left by the inflection of the walls in the hind part of the hoof. The bars are the inflected portion of the wall running forwards under the foot so as to form an acute angle, within which the frog lies.

The fore and hind feet are in a general way similar, but the hind feet are narrower and rather more upright.

The periople is the epithelial varnish covering the external surface of the wall, and thickest at the top of the wall where it forms the periople ring.

Inside the wall, which consists of horny laminae, are the sensitive laminae.

The coronary cushion is a prominent ring arranged round the edge of the hoof. It is lodged in a special groove in the horn, termed the cutigeral groove. The coronary cushion is continuous with the keratogenous membrane, a highly vascular structure (like the cushion). This membrane is directly inside the sensitive laminae, which themselves dovetail into the insensitive laminae of the hoof without.

The plantar cushion is a fibroelastic pad containing fatty tissue and few vessels. It is continuous with the coronary cushion. It is sometimes called the 'sensitive frog' and rests upon the frog or foot-pad. The sensitive sole is the part above the horny sole.

The principal functions of the foot are three, (1) wear and tear, (2) supporting weight, and (3) warding off concussion. The plantar cushion is especially constructed for the last of these functions, but in common with the vascular part generally it produces the horn which goes to form the hoof.

The foot contains three bones, the os pedis or coffin bone, the navicular which rests slightly on the os pedis and is held in position by ligamentous tissue, and the os coronae, which only partly belongs to the foot. Above the os coronae, is the os

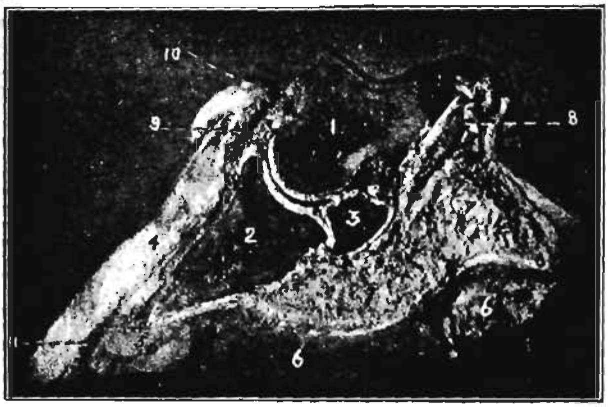


Fig. 57. Horse's Foot (from Smith, Messrs Baillière, Tindall and Cox). 1. os coronae. 2. os pedis. 3. naviculae. 4. wall. 5. sole. 6. frog. 7. plantar cushion. 8. perforans tendon. 9. wall-secreting substance. 10. extensor pedis tendon. 11. junction of wall and sole.

suffraginis which articulates with the cannon bone, but neither of these bones belong to the foot. The pedal bone does not occupy the whole of the interior of the hoof but its place is taken on either side by a plate of lateral cartilage. The two lateral cartilages which reach high above the level of the hoof are attached to the pedal bone.

The navicular supplies a yielding articulation to the os coronae, since the latter bone rests partly on the navicular and only partly on the pedal bone. A direct concussion of the pedal

joint is thereby avoided or at any rate reduced, for although the force of the body weight is partly transferred to the pedal bone on which the navicular rests, the latter bone yields under pressure, as does also the pedal bone.

The chief support of the navicular is the perforans tendon which passes beneath it, and so admits of the yielding articulation just mentioned. There is a synovial apparatus[1] attached which serves the purpose of reducing the friction. Nevertheless the navicular bone owing to the important part it plays, and its exposure to compression, is very liable to disease, and any inflammatory condition set up is likely to spread to the perforans tendon and other adjoining parts.

We may now consider more closely the structure and functions of the hoof and the horn producing tissues, and the relation of these parts to one another.

The keratogenous membrane has upon its outer surface a large number of leaves which constitute the sensitive laminae. These leaves are longer at the toe than at the heel where they are short and turned in to form the 'sensitive bars.' The keratogenous membrane is devoted to leaf formation excepting on its inner surface which encloses the pedal bone.

The coronary substance extends all round the coronet. The periople is secreted from that part of it which occupies the cutigeral groove between the upper margin of the hoof and the skin. On its lower edge the coronary substance fuses with the fibres from the sensitive laminae, being continuous with the keratogenous membrane as already stated.

The insensitive foot or hoof covers the sensitive part completely. The foot is covered by the periople which is a varnishing substance secreted in the coronary region where it is thickest. It gradually gets thinner lower down the hoof. Its function is to cement the junction of the skin to the hoof and also to control evaporation from the hoof.

The colour of the wall is black or buff, the pigment being produced in the coronary substance.

The wall is thicker at the toe than at the heel, since at the toe

[1] This is commonly called the navicular bursa, but its function appears to be to lubricate the bone and parts concerned, and not merely to act as a cushion, like the bursae over which the extensor pedis and other tendons pass. These are little closed sacs and are so placed as to protect the parts from injury.

which is the final propelling part of the foot the friction is greatest. The base being in reality the inflected portion of the wall are, like the rest of the wall, intended to bear weight. The inflection admits of there being room for the elastic portion of the foot (the plantar cushion).

The sole is normally concave. As a practical matter it cannot be too thick. While the wall can go on growing indefinitely the sole cannot, since after a certain degree of growth the horn fibres become disintegrated and scales are shed. The junction of the sole and wall is marked by a white line where the horn is softer. The function of the horny sole is to provide protection for the sensitive structures within; its concave surface does not adapt it for carrying weight, excepting at the edge where it is connected with the wall.

The foot-pad or frog is moulded on the plantar cushion. The horn of which it is composed is markedly elastic and contains a relatively large amount of moisture. Like the sole it casts out scales. The frog serves as an anti-concussion mechanism, for the impacts it receives are transferred to the plantar cushion and thence to the lateral cartilages and wall of the foot which are stretched outwards. The frog normally comes into contact with the ground, and if this is not the case it is liable to disease. In hot dry climates the horny parts of the foot, especially of the frog, tend to become excessively hard and to cause lameness from bruising the underlying sensitive structures.

The Structure of the Horn. The horn of all parts of the hoof consists essentially of keratinised epithelial cells which are spindle-shaped, oblong, or irregular. They contain nuclei, granular matter, and very often pigment, and are united by a cement substance. The horn substance is soluble in caustic alkali, and consequently horses should not to be allowed to stand in their own urine.

The horn structure in the progress of its development acquires canals or tubes which are used as a system of irrigation through which the hoof is supplied with the moisture necessary for preserving a proper elasticity. Without this moisture the horn substance crumbles. Evaporation from the substance is regulated by the periople as already mentioned, but nevertheless it is constantly taking place in some degree. In shoeing it is important to avoid injury to the periople as much as possible. The elasticity

of the hoof is an essential quality, as without it the structure would no longer act as an anti-concussion mechanism.

The actual horny material is a protein of the following approximate composition:

C	51·51
H	6·96
N	17·46
O	19·49
S	4·23

Salts (chlorides, sulphates, and phosphates of sodium, magnesium, iron and silicon) are present in small amounts. The quantity of water is variable. The foot-pad contains the most and the wall the least.

The laminae of the hoof are attached at the antero-lateral part to bone, at the remaining parts to cartilage. The lateral cartilages supply a movable attachment to the sensitive laminae, and admit of their passing outwards. The lameness resulting from side-bone (or ossification of the lateral cartilages) is due to the sensitive structures within being squeezed between the pastern bone and the ossified cartilage.

The laminae of the hoof are much folded, and their entire surface if spread out has been estimated at from 8 to 10½ feet.

Inflammation of the laminae occurs as a result of various causes. It may be due to overwork, or it may be due to a horse standing too long in one position when the laminae tend to become congested. Such a tendency may be overcome by exercise which relieves the congestion by causing the blood to circulate. This is one of the recognised modes of treatment for laminitis or founder. This disease frequently results in separation of the horny and sensitive laminae, and may be followed by descent of the coffin bone.

The chief anti-concussion mechanisms may now be summarised as follows: (1) the yielding articulation of the coffin bone, (2) the increase in the width of the foot when the heels come to the ground (the process being one of expansion), (3) the elastic foot-pad or frog, and (4) the slight up-and-down play between the pedal bone and the sublaminal tissue as the weight is removed from or comes on the foot. This latter movement is participated in also by the horny sole.

Shoeing. The following points have been emphasised by Smith in regard to 'physiological shoeing':

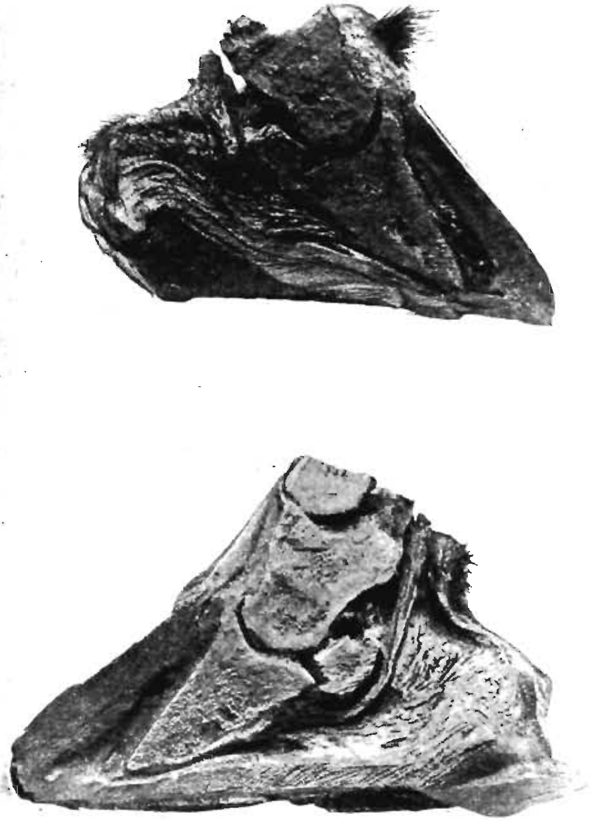


Fig. 58. Displacement of the coffin bone. (The lower figure represents the normal condition.)

(1) Reduction of the wall to its right proportions such as would have occurred through friction had there been no shoe.

(2) Fitting the shoe accurately to the outline of the foot and avoiding rasping which destroys the periople, and so renders the horn brittle.

(3) Leaving the sole intact since it cannot be too thick.

(4) Leaving the bars intact since they are part of the wall and are intended to bear weight. (The shoe should rest on them.)

(5) Leaving the foot-pad intact. (This should be level with the ground surface of the shoe.)

(6) The pattern of the shoe is immaterial, so long as it has a true and level bearing and rests firmly upon the wall and bars.

(7) The shoe should be secured with as few nails as possible, so as to avoid any unnecessary destruction of the horn. Moreover the nails should not be driven in high up as this is disastrous to the feet.

Chestnuts and Ergots. The chestnuts (wrist and hock callosities) are horny excrescences on the inside of the horse's forearms and hocks. The wrist callosities are the biggest, but in horses belonging to the heavy breeds the hind chestnuts are also

Fig. 59. Chestnut (hock callosity) on right hind leg of pony of cart-horse type (from Ridgeway).

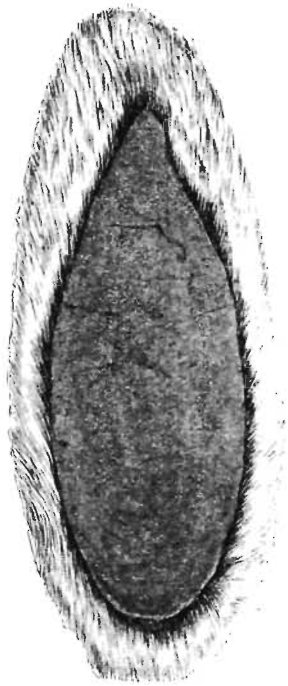


Fig. 60. Chestnut in right fore leg of Prejvalsky horse (from Ridgeway).

large. In ponies of the 'Celtic' type (e.g. Hebridean or Iceland ponies) the hind chestnuts are generally absent. They are also absent in some Arabs and other 'well bred' horses (e.g. in North African horses and occasionally in Thoroughbreds). The asses and zebras also have no hind chestnuts.

The ergots are excrescences of a similar character and occur on the back of the fetlock in nearly all equine animals. They are, however, absent in Celtic ponies and sometimes in Arabs and Thoroughbreds (i.e. in those breeds which tend to lack hock callosities).

Fig. 61. Chestnut (hock callosity) on right hind leg of Prejvalsky horse (from Ridgeway).

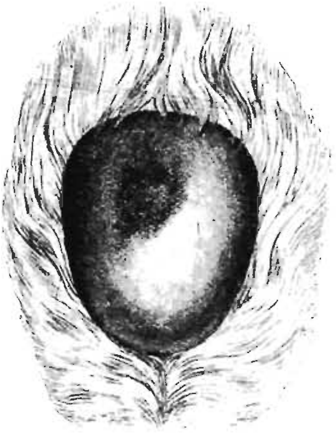


Fig 62. Ergot on hind leg of ass (from Ridgeway).

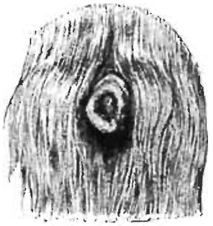


Fig. 63. Ergot on right fore leg of Arab (from Ridgeway).

The Hoof in Ruminants and Pigs. In the ox, the sheep, and pig, the hoof has the same essential structure as in the horse but has no frog and no lateral cartilages. It is, however, cleft

into two portions corresponding to the two digits (the 3rd and 4th, the horse having only one digit, the 3rd). The cleft between is called the inter-digital space.

Exostoses.

When the fore leg of a horse descends upon the ground it is necessarily straight; otherwise the foot could not be put down flat, or heel first, as happens in fast pacers. Since the limb is rigid (the knee being quite straight) the force of concussion is greatest nearest the ground where the impact occurs, and gradually diminishes as it ascends the leg. As has been shown above, there are numerous devices present in the foot for reducing the shock caused by the impact, and not the least of these are the presence of the foot-pad or frog, the laminae of the hoof, and the yielding articulations of the foot and fetlock joints. In the case of the hind limb the shock of concussion is partly provided against by other means. Here instead of the limb being straight, it is bent at the hock, and the impact is felt more especially at this point.

Since these facts have a direct bearing on the causes of the various sorts of exostoses or pathological outgrowths of bone which are so common in horses under domestication, it is not out of place to give some account of them in dealing with the physiology of locomotion.

In view of the facts stated above it is not surprising that the hock is more frequently affected with disease than is the knee. In the case of bog spavin there is no bony outgrowth, but merely an enlarged condition due to the distention of the joint capsule by an abnormal quantity of synovial fluid which collects there in response to strain. It occurs most commonly in cart-horses, and especially in Clydesdales, whose hocks stand out far behind. It is generally the result of severe exertion or overstrain, but it does not as a rule cause lameness. In bone spavin or true spavin there is a genuine exostosis usually on the internal side of the hock joint. This growth of bone is the result of inflammation, but the precise point of origin of the inflammation (whether it is in the articular cartilage or in the membrane covering the ends of the bones or elsewhere) is not clear. Spavin nearly always causes lameness. It is frequently followed by anchylosis[1] of one

[1] Fusion of two or more bones which normally are capable of separate movement.

or more of the joints composing the hock. It is commoner in comparatively young than in old horses, and particularly in those having weak or ill-shaped hocks which are placed too far back or taper off too much towards the lower extremity. It occurs as a result of high hock action on paved or hard roads, and in Hunters may be caused by the strain of jumping. When anchylosis has taken place lameness frequently ceases, so that the hastening of anchylosis should be the aim of all treatment.

Fig. 64. Photo of spavin.

Sometimes however the inflammatory action extends to the astragalus and damages the articular cartilage of the true joint. These cases are incurable.

Splints generally occur on the side of the cannon bone of the fore leg, or between the cannon and splint bones. They are much more common on the inside of the limb and are generally restricted to the upper third of the bone. They may occur so high as to involve the knee joint, causing lameness. They are not so common in the corresponding positions on the hind leg but may occasionally occur. Like other exostoses they result from inflammation. They are sometimes brought about

by external injuries, but are more frequently due to high knee action causing much concussion in horses driven or ridden on hard roads. Thus city horses are more prone to splint than horses in the country. Splints do not necessarily cause lameness, but are more likely to do so when the inflammation is starting, and if the knee joint is affected

Fig. 65. Photo of splint.

Ring-bone is the name given to any exostosis occurring on the pastern or coffin bones; if involving either of these joints it is termed a true ring-bone; in other positions it is a false ring-bone. It occurs more commonly on the front aspect of these bones and may extend completely around them. It is commoner and more liable to cause lameness on the fore limbs. It is often associated with upright pasterns. Heavy horses are more disposed to it than light ones. When we consider the

amount of pressure which must inevitably affect the pastern bones, it is easy to understand how an inflammatory condition is liable to arise in this region. Ring-bone often occurs in association with fractured pasterns, and may result from such causes as galloping on a hard road or on an irregular ground surface.

Fig. 66. Photo of ring-bone.

Side-bone or ossification of the lateral cartilage is common in cart-horses with straight pasterns. It may result from hard work or from going faster than the normal, as with heavy draught horses when made to trot, or with light horses when over-driven. Side-bone is frequently associated with ring-bone. The lameness which results from side-bone is due to the sensitive structures being squeezed between the fetlock bones and the ossified cartilage.

Besides the kinds of exostosis just described, osseous outgrowths may arise in other parts through inflammation induced by injury as by a horse falling or hitting 'timber' when hunting.

Fig. 67. Photo of side-bone.

Voice-Production.

Before concluding this chapter it may be well to consider briefly the mechanism employed by animals in voice-production.

The larynx as described in an earlier chapter is a chamber with cartilaginous walls and situated at the upper or anterior end of the trachea, with an aperture (the glottis) communicating with the mouth. It contains two elastic cords—the vocal cords

—approximating to one another in a V-shape. The respiratory and vocal movements necessitate the opening and closing of the angle within the V, and this is effected by the muscles of the larynx. The walls of the glottis are also moved by dilator (abductor) and constrictor (or adductor) muscles, and these are used both in respiration and in phonation. The muscles which relax the vocal cords or render them tense are exclusively phonatory muscles. The chief changes which the larynx undergoes in voice-production relate to the cords, the mouth, pharynx, nasal chambers, participating in the sound produced to a greater or less extent.

Neighing in a horse is an expiratory sound, and is produced partly by the mouth and the nostrils. Braying in an ass is said to be partly inspiratory and partly expiratory. Bleating and bellowing (in sheep and cattle) are expiratory, the mouth participating. Yawning is a deep inspiration succeeded by an expiration. Coughing and sneezing are exclusively expiratory.

'Roaring' in a horse is a diseased condition due to the paralysis of one of the abductor muscles of the larynx, and almost invariably occurs on the left side only.

CHAPTER XI

THE DUCTLESS GLANDS AND THE ORGANS OF INTERNAL SECRETION

The term 'Internal Secretion' was first used by Claude Bernard who applied it to describe the glycogenic function of the liver. This gland, as has already been recorded, stores up carbohydrate as glycogen and secretes it into the blood, as required, in the form of sugar. The liver, then, in addition to being an externally secreting gland (that is to say, a gland which elaborates substances (in this case bile) which are discharged outwards through a duct) is also an internally secreting gland. In one sense all the organs and tissues of the body are internally secreting organs since the substances which pass out from them into the circulating blood are different from the substances which pass in. But the term 'internal secretion' is usually restricted to those cases where the substances elaborated by the organs in question have a precise function and act upon other organs or tissues in the body in a definite way. The internally secreting organs therefore are those which produce 'hormones' or chemical excitants which after being carried throughout the body in the blood stream promote the secretion of particular glands or the growth of particular tissues for which they have a specific action. Thus, the liver although it is in a very literal sense an organ of internal secretion is not ordinarily included in that category, since it does not elaborate any bodies included under the term hormone.

We have already dealt with typical hormones in describing the mechanisms of pancreatic and gastric secretion, the chemical excitants in these cases being secreted by the wall of the duodenum and the pyloric end of the stomach respectively. We have seen also that the waste product carbon dioxide may be regarded as of the nature of a hormone, since when its tension in the blood reaches a certain point, it has a specific exciting action upon the respiratory centre in the medulla, thereby quickening the respiratory movements. It is possible that the

other hormones of the body may have arisen in evolutionary development as waste products, and that the organs and tissues on which they now act may have only gradually learnt to respond to their presence in the progress of phylogeny (i.e. the development of the race). However this may be the functional correlation existing between certain often distantly situated organs has become very perfect as the examples already given and described below sufficiently demonstrate.

The Pancreas. It has been shown by von Mering and Minkowsky that extirpation of the pancreas is followed by the appearance of sugar in the urine even though carbohydrate is excluded from the diet. At the same time the quantity of urine excreted tends to increase, the percentage of urea is greater, acetone makes its appearance, there is an abnormal hunger and thirst, and these symptoms are associated or followed by emaciation ending in death. Retention of one-fourth or one-fifth of the total normal amount of gland tissue is sufficient to prevent glycosuria. Moreover, the connection of the pancreas with the duodenum may be cut off, and yet there is no glycosuria. It has been stated also that grafting of pancreatic tissue under the skin may stop these symptoms from appearing after the removal of the whole gland from the normal position. Ligature of the pancreatic duct does not cause glycosuria, though the gland excepting for the islets of Langerhans undergoes atrophy. It has been concluded therefore that the pancreas elaborates an internal secretion, probably in the islets of Langerhans, which in some way regulates the glycogenic function of the liver, and that without this secretion the liver is no longer able to store up glycogen but discharges it as sugar into the blood whence it is excreted by the kidneys. The pancreas therefore, is an example of an externally secreting gland (i.e. a gland provided with a duct) which is at the same time an organ of internal secretion, and this secretion is essential for the maintenance of the life of the animal.

The Thyroid. The thyroid proper is represented by two oval bodies lying one on each side of the trachea at its junction with the larynx. It is composed of vesicles filled with a colloid substance and bounded by a cubical epithelium, the vesicles being separated by connective tissue containing vessels.

Schiff found that extirpation of the thyroid in dogs led to death in from one to four days. Previous to death the animals

showed muscular tremors, convulsions and emaciation. Similar results occur in people afflicted with thyroid insufficiency. The diseases due to this cause are known as cretinism and myxoedema. The former of these occurs in children and is common in certain parts of Switzerland but is not very infrequent in other countries, including England. The individuals, who are known as cretins, suffer from greatly arrested growth and deficient mental development which may be very marked. Myxoedema, which affects persons of mature age, is a disease of a similar character. The symptoms are loss of hair, nervous and mental deterioration, and loss of memory which if not relieved by treatment are followed by premature death. The recognised treatment is

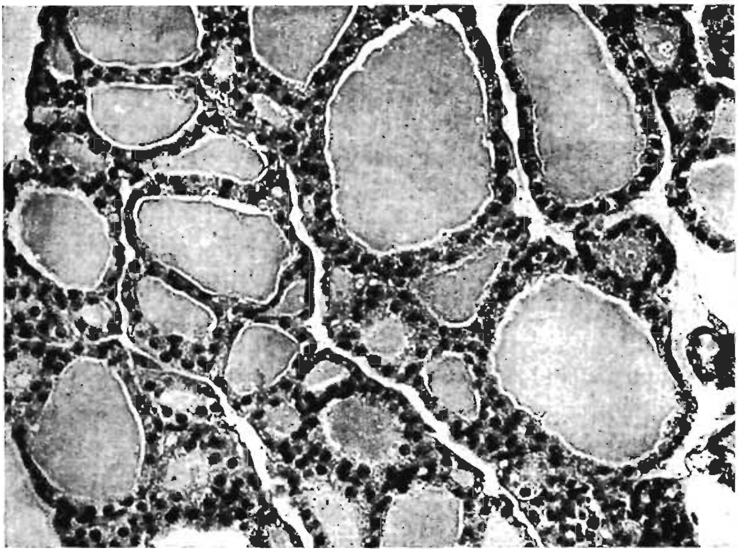


Fig. 68. Section through thyroid gland (from Schafer).

feeding on raw thyroid gland or on extract, the glands being obtained from cattle or sheep. Thus the active substance of thyroid is presumably the same in all mammals, and it can be absorbed unaltered through the wall of the alimentary canal. Feeding on thyroid gland removes or greatly mitigates the symptoms due to cretinism, while myxoedema can often be completely cured. It is necessary however that the treatment should be continued permanently, otherwise the patient lapses into the

state of disease, since the thyroid which is administered merely takes the place of the secretion provided by a normal thyroid and has no influence in restoring the diseased organ to a healthy condition. Some animals do not appear to suffer any harmful effects from removal of the thyroid glands. Thus adult sheep seem to remain unaffected. If however the thyroids are extirpated from young lambs they become typical cretins and cease to grow. This has been shown by Sutherland Simpson. Thyroid grafts if successfully implanted may be as successful as feeding with extract, but if the graft does not become permanently

Fig. 69. Thyroidectomised or cretin sheep aged 14 months with normal sheep of same age (after Sutherland Simpson from Schafer).

'established' the beneficial effect continues only so long as the transplanted tissue persists. The active principle of the thyroid gland has not been isolated, but a substance called iodothyrin which contains 9·3 per cent. of iodine has been prepared, and this is said in some measure to counteract the evil results following upon removal of thyroid. Accessory thyroid tissue is sometimes found posterior to the normal position of the thyroid, and this may hypertrophy and compensate for the extirpated glands.

The Parathyroids. Normally there are two parathyroid glands on each side; sometimes they are embedded in the thyroid tissue but more generally they are situated just outside. Accessory parathyroids are not uncommon. Unlike the thyroids proper the parathyroids are composed of solid masses of rounded cells and contain no vesicles. It is said however that after thyroidectomy the parathyroids may develop a vesicular structure and even take the place of the thyroids proper. Extirpation of the parathyroids without the thyroids induces tonic muscular contractions or tetany, and the injection of parathyroid extract relieves the condition. It is suggested that many of the effects of thyroid removal may in reality be due to the extirpation of the parathyroids since it is not easy to remove the former organs without destroying the latter ones.

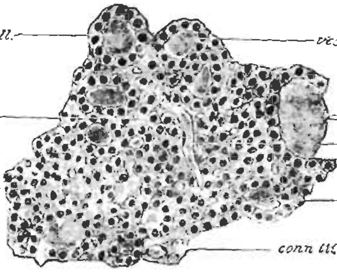


Fig. 70. Section through parathyroid. *bld. v.* blood vessel (after Vincent and Jolly), *coll.* colloid, *conn. tis.* connective tissue, *epith. c.* epithelial cell, *ves.* vesicle.

The functions of the thyroids and parathyroids are still only imperfectly understood. They appear to exercise a profound influence on the nervous system and on the nutrition of the whole body, but how much of this influence is due to the thyroids and how much to the parathyroids is uncertain. Moreover the age of the animal is a factor in the results produced, and these are not the same for all species of animals.

The disease known as goitre is an enlargement of the thyroid and the condition produced may be one of either hypothyroidism or hyperthyroidism. In the case of endemic goitre, notwithstanding the enlargement of the gland the symptoms are those of hypothyroidism. In the case of exophthalmic goitre or Grave's disease, the condition is apparently the result of hyper-secretion.

for some of the symptoms can be induced by the excessive administration of thyroid extract. The most obvious symptom is the protrusion of the eye-ball, this being accompanied by rapid and irregular cardiac action, nervous excitation, and an increased metabolism.

The Suprarenal Bodies. These bodies are situated one on each side just in front of the kidney. Accessory suprarenals

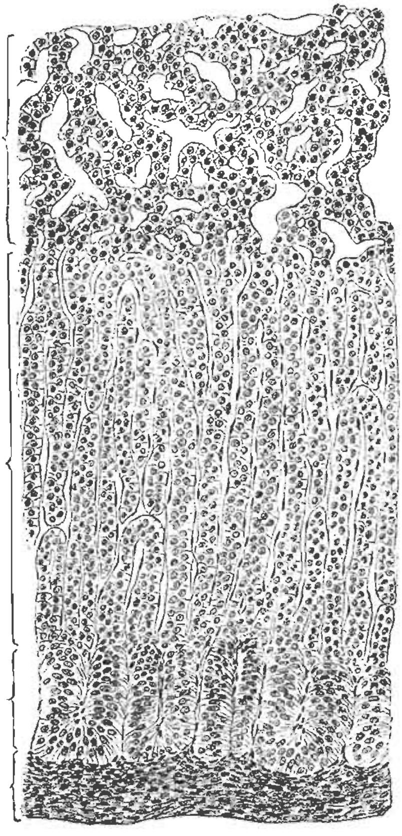


Fig. 71. Section through suprarenal gland of dog (after Böhm and Davidoff from Schafer).

are not uncommon. Each gland has a capsule of connective tissue giving off strands into the interior, a yellow cortex consisting of parallel rows of cells, the long axis of each row or column being at right angles to the surface, and a dark red medulla consisting of a mass of irregularly arranged cells with blood vessels.

Brown-Séquard showed that removal of the suprarenals caused death in shorter time than removal of the thyroids. The symptoms preceding death were great muscular weakness, intense prostration, and loss of vascular tone. These are the symptoms of Addison's disease which is a disease of the suprarenals. Oliver and Schafer showed that extract of these organs when injected into the circulation causes a very marked rise of blood pressure, caused by the contraction of the peripheral arteries. If the vagi are then cut or paralysed, the heart's action is enormously accelerated and strengthened. Elliott and others have shown that the extract acts upon the sympathetic fibres of the vessels, and there is a special connection (developmental as well as functional) between the suprarenal medulla and the sympathetic system. The effect of suprarenal extract in constricting the arteries is taken advantage of by surgeons and others to stop bleeding or inflammation, but in the latter case the effect is transient and continues only so long as the active principle is present.

The active principle of the suprarenal glands is called adrenalin. It is produced only by the medulla, the function of the cortex being problematical. Adrenalin has the empirical chemical formula $C_9H_{13}NO_3$. It was first synthesised by Takamine and Aldrich. It is of the nature of a hormone and is necessary for the normal metabolism of the muscles on which it acts through the sympathetic nervous system. Absence of the secretion causes loss of muscular tone and vigour, as exhibited by the muscles of the heart and vessels and by the skeletal muscles.

The Pituitary Body. This small organ lies at the base of the third ventricle of the brain with which it is connected by a short hollow stalk, the infundibulum. The stalk is formed of nervous tissue, and enlarges in the interior of the pituitary body becoming the pons nervosa. In front of the pons nervosa is an epithelial portion constituting the anterior lobe or pons anterior. It contains numerous vessels. Between this and the pons nervosa is another epithelial portion, the pons intermedium, which is only slightly vascular. The pons nervosa and the pons intermedium together form the posterior lobe. The pons nervosa is the least vascular part of the pituitary.

No active principle has been extracted from the anterior lobe. Nevertheless there is evidence that this lobe plays an important

rt in metabolism. Thus tumours growing on the anterior be are often associated with acromegaly (or overgrowth of the ones of the face) and gigantism (or overgrowth of the bones of e limbs, the epiphyses not ossifying). These diseases are hought to be the result of hyperpituitarism. On the other hand ituitary tumours may produce an atrophy of the gland and so e a cause of hypopituitarism.

Active extracts containing hormones have been obtained rom the posterior lobe. Thus Howell found that there was hormone which acted on the heart and vessels, causing a reat rise of blood pressure, strengthening the heart beats and onstricting the arteries. Schafer and Herring found that osterior lobe extract has a diuretic effect on the kidneys; Weed nd Cushing ascertained that the extract has a stimulating action n the flow of the fluid of the cerebro-spinal canal; and Ott and cott discovered the galactogogue effect of extract of posterior be (see p. 198). It would appear therefore that the pituitary roduces several hormones each having its characteristic function, ut none of these have been isolated.

The Pineal Body. This is a very small glandular organ ituated on the dorsal surface of the third ventricle. Its functions ave not been ascertained, but it has been found that injection f pineal extract has a slight galactogogue action.

The internal secretions of the generative glands are more onveniently treated of in the chapters dealing with these organs.

The Inter-Relation of the Organs of Internal Secretion. There is considerable evidence of a functional inter-relation f certain of the organs of internal secretion with one nother, but the whole subject is very obscure. It has been scertained that removal of the thyroid leads to hypertrophy of he pituitary, but it is not very apparent whether the growth is ompensatory or whether the two organs are antagonistic. Colloid substances tend to arise in the pons anterior of the ituitary after thyroidectomy, and there is an increased activity n other portions of the gland. There is also some relation etween the suprarenals and thyroids since thyroid secretion ppears to promote suprarenal activity, while thyroidectomy iminishes the secretion of the suprarenals. Again, extracts of uprarenal medulla and pituitary posterior lobe seem mutually o facilitate each other's action on the vessels. The connection

between the thyroids and parathyroids has already been remarked on, and the inter-relation of the ductless glands and the sexual organs will be touched upon in the succeeding chapters. Whether or not there is any true compensating mechanism between internally secreting organs of various kinds is a very open question, but it is abundantly clear that such relation exists between organs of the same kind. Thus, removal of one suprarenal may be followed by compensatory hypertrophy of

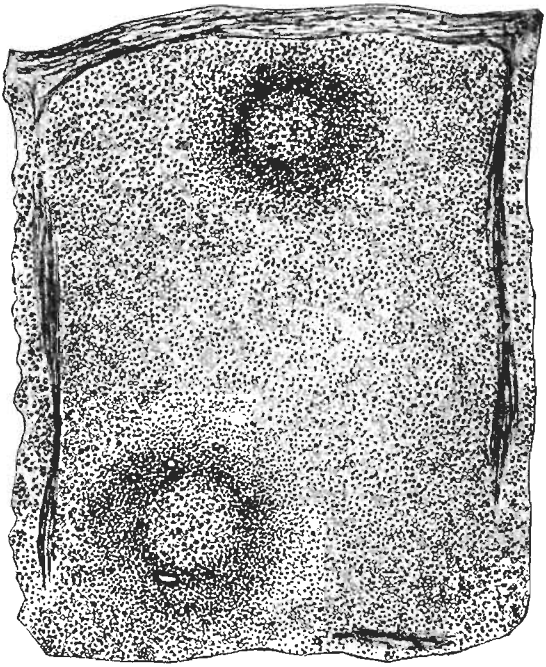


Fig. 72. Section through spleen showing Malpighian corpuscles (*from Schafer*).

the other (just as happens in the case of the kidneys), and often after extirpation of the main internally secreting organs of a particular kind (e.g. the thyroids) accessory glands may hypertrophy and assume the functions of the glands removed.

In addition to the ductless glands described above there are certain others which so far as known do not elaborate hormones. Of these the most noteworthy are the spleen and the thymus.

The Spleen. This organ is enclosed within a capsule which

is partly fibrous and partly muscular, and some of the muscular tissue projects into the interior of the organ in the form of trabeculae. These trabeculae constitute a sort of framework in which the typical spleen tissues lie. The spleen is essentially a haemolymphatic gland, that is to say, a gland composed of lymphoid tissue but containing also a large number of erythrocytes, some of which are in a state of partial or complete disintegration. It differs from other haemolymphatic glands in possessing Malpighian corpuscles or nodules densely packed with lymphocytes, each nodule surrounding an arteriole. Apart from the vessels contained within the Malpighian corpuscles, all the arteries communicate directly with the tissue elements of the

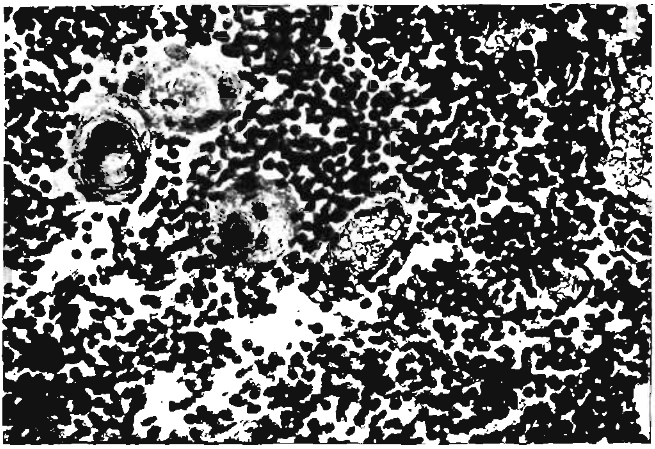


Fig. 73. Section of thymus showing Hassal's corpuscles (from Schafer).

spleen, and from this tissue the blood is gathered up anew so as to flow into the splenic vein.

The functions of the spleen are problematical. It can be removed without the animal appearing to incur any harm, but this may be due to other haemolymph glands (of which there are often many scattered about the alimentary region) taking on the splenic functions. It is known that the spleen is concerned to some extent with the destruction of red corpuscles, and that it contains a considerable amount of iron. It is also known that in common with other lymphatic glands the spleen produces leucocytes, and that uric acid is present in it in some quantity.

Beyond these facts nothing can be stated definitely regarding its utility to the organism, but according to some authorities it is also a factory for erythrocytes.

The Thymus. This organ is composed of lymphoid tissue closely packed in the cortex but less dense in the medulla. The latter contains the concentric corpuscles of Hassal which are epithelial cells arranged in rings and are specially characteristic of the thymus. Their significance is unknown. The organ is usually situated on the ventral surface of the great vessels communicating with the heart, but in some animals (e.g. guinea-pigs) the thymus bodies are placed much further forward in the neck. The thymus normally atrophies about the age of puberty. Its functions are very obscure, and its removal appears to be followed by no harmful results. It seems probable however that after extirpation the functions of the thymus are taken over by other lymphatic glands.

CHAPTER XII

THE MALE GENERATIVE ORGANS

The spermatozoa or conjugating cells produced by the male are developed in the testicles which are therefore the essential reproductive organs in that sex, just as the ovaries which produce the ova are the essential reproductive organs in the female sex. The epididymis, vas deferens, urethra and penis which are instrumental in conveying the spermatozoa to the exterior, together with the various glandular structures which communicate with them, may be described as the accessory male generative organs.

The Testicle. In man and in all the domesticated animals the testes (or testicles) are a pair of glands lying outside of the body cavity in the scrotum which is situated posteriorly between the anus and the urogenital opening. The scrotum consists of a pair of pouch-like sacs communicating with the body cavity by the inguinal canals through which the spermatic cords and vasa deferentia pass. The spermatic cords contain the blood vessels and nerves which supply the testes, and the vasa deferentia are the ducts which convey the testicular secretion to the urethra or common urogenital canal.

In the lowest group of mammals (Monotremata) the testes remain in the body cavity always as they do in birds. In Insectivora (e.g. the mole) the testes descend periodically into temporary receptacles, and there is no true scrotum. In many rodents the testes after descending into the scrotum at the commencement of rut are withdrawn into the body cavity at the end of the period. In most other animals the testes after descending into the scrotum during early life (and generally before birth) remain there permanently, but it is noteworthy that in the ram after tupping the organs apparently become smaller and tend to be drawn upwards without however passing into the cavity of the abdomen.

Each testis is surrounded by a serous membrane (the tunica vaginalis) within which is a fibrous capsule (the tunica albuginea). Posteriorly the fibrous capsule is prolonged into the interior of the gland to form the mediastinum testis. The greater part of the

organ is composed of the seminiferous tubules which are separated from one another by epithelioid interstitial cells (see p. 164). The tubules contain several layers of epithelial cells supported externally by a basement membrane. On the internal surface of the basement membrane are the spermatogonia. Certain of the

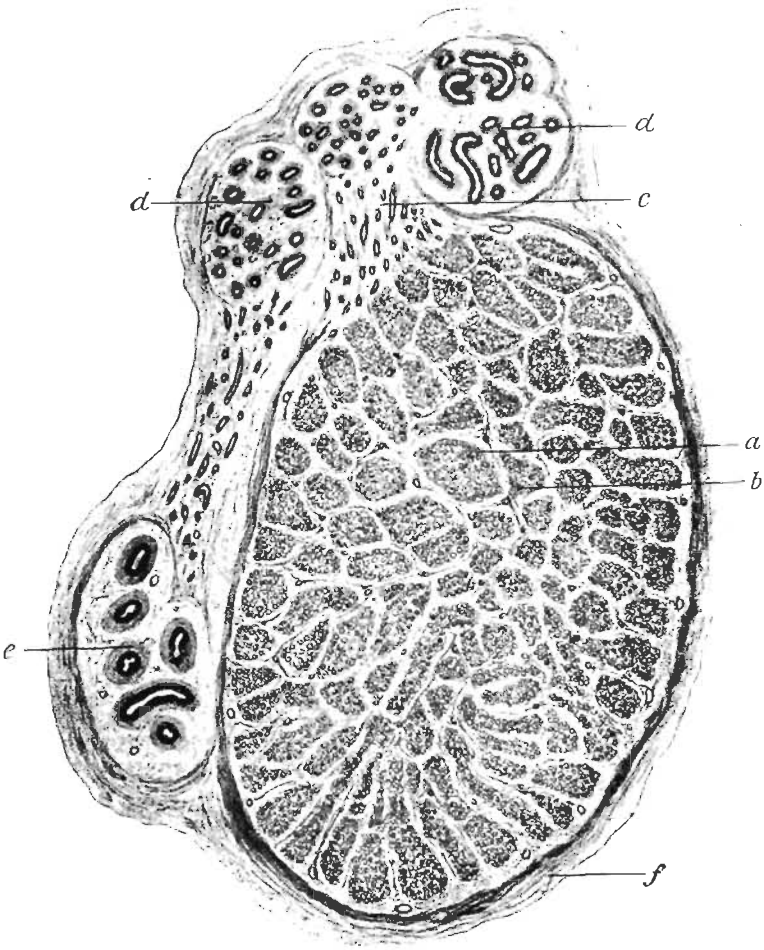


Fig. 74. Section through testis (from Marshall). *a* seminiferous tubules, *b* interstitial tissue, *c* rete testis, *d* vasa efferentia, *e* vas deferens, *f* tunica albuginea.

epithelial cells between the spermatogonia are enlarged and project among the more internal cells in association with developing spermatozoa. These are the cells of Sertoli. They are believed to

have a nourishing and supporting function. On the inside of the spermatogonia are certain larger cells known as spermatocytes. They are the products of division of the spermatogonia. On the inside of the spermatocytes are the spermatids which are derived from the spermatocytes by cell division. The spermatids in many cases become elongated and converted into spermatozoa. A small quantity of fluid is secreted into the testicular lumina, but it does not appear to be certain as to what cells are especially concerned in this secretion.

A fully developed spermatozoon consists of an egg-shaped head which represents the cell nucleus, a short cylindrical body or middle piece, and long delicate vibratile tail, by means of which the sperm is propelled forwards.

Fig. 75. Spermatozoon of ram (from Marshall).

In the process of spermatogenesis the quantity of nuclear material (as shown by the number of chromosomes or filaments which go to compose the nuclear material) in each final product of division (i.e. in each spermatozoon) is reduced to one-half of the normal amount characteristic of the cells in the species in question. Thus in the horse the normal number of chromosomes for all the cells of the body excepting the mature reproductive cells is 26, whereas the number of chromosomes in the spermatozoon of the horse is 13. This is due to the fact that in the last cell division but one leading up to spermatogenesis the chromosomes do not undergo the splitting which universally characterises cell-division excepting in the reduction processes of the reproductive cells. In the final division the chromosomes split as usual. The nuclear material in the mature ovum is also reduced by half, so that in the act of fertilisation when the ovum and spermatozoon unite the number of chromosomes becomes once more restored to the normal amount characteristic of the species.

The efferent ducts of the testis or vasa efferentia (about twelve in number) open into a single convoluted tube situated at the posterior end of the testis. This is the *epididymis*. It is lined internally by a columnar, ciliated epithelium which is believed to have some secretory activity. The epididymis serves mainly as a storehouse for the spermatozoa prior to seminal ejaculation. Smooth muscle fibres are present in its walls as well as in those of the vasa efferentia.

The *vas deferens* is the duct conveying the seminal fluid in which the spermatozoa pass from the epididymis to the urethra. It is lined internally by a non-ciliated columnar epithelium, and its wall contains several layers of smooth muscle fibres.

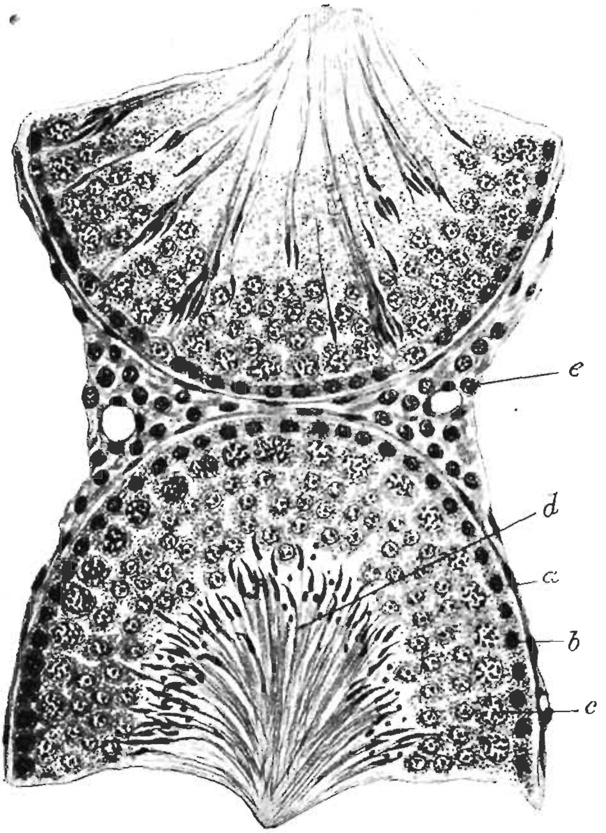


Fig. 76. Section through seminiferous tubules (from Marshall). *a* basement membrane, *b* spermatogonium, *c* spermatocyte, *d* spermatozoa in cavity of tubule, *e* interstitial tissue containing blood vessels.

The Accessory Glands. The semen or fluid discharged through the penis in an ejaculation, is the secretory product of the testis, epididymis, vesiculae seminales and other accessory glands. Near the termination of the vas deferens there is a small sac, the *ampulla of Henle*, which also contains small secretory glands but according to Disselhorst its chief function is to act as a seminal reservoir.

He suggests that there is a relation between the size of the ampulla and the time occupied by coition, stating that in dogs, cats and boars where coition is a slow process the ampulla is small or absent, whereas in horses and sheep where coition occupies a relatively short time the ampulla is well developed.

The *vesiculae seminales* are situated at the ends of the vasa deferentia. They are provided with a glandular epithelium, outside of which are thin muscular layers. It was formerly supposed that they were of the nature of seminal reservoirs, but even in the hedgehog, in which these organs undergo a very great development at the breeding season, it has been impossible to find spermatozoa in the vesicular fluid. On the other hand they contain a large quantity of glairy, milky fluid with much crystalloid material, which Hopkins has shown to consist of a phosphoprotein. The precise function of the vesiculae must still be regarded as undecided. It would seem probable that one of their functions is to dilute the semen and so assist in providing a medium for the transference of the spermatozoa.

The prostate is a tubular gland surrounding the urethra at the base of the bladder. It communicates with the urethra by numerous small ducts. Associated with the glandular tissue are a number of smooth muscle fibres, and there is an abundance of vessels supplying the gland. The prostatic secretion is viscid. It contains proteins and salts, and is sometimes very slightly acid in reaction. In old subjects concretions are frequently present in the gland. Concerning the function of the prostatic fluid nothing definite is known. It has been suggested that it assists in providing the spermatozoa with nutriment, and it is obvious that it contributes additional fluid to the semen. It is not improbable that one of its main functions is to cleanse the urethra of urine prior to the ejaculation of spermatozoa, for it has been ascertained that in a normal seminal ejaculation in the horse the first fluid to be discharged contains no sperms and is almost certainly chiefly of prostatic origin.

Cowper's glands are a pair of small tubulo-racemose glands situated near the anterior end of the urethra with which they communicate by two ducts. The glands are lined internally by a secretory epithelium. The significance of the viscous secretion which the glands produce is obscure. Possibly they serve the same function as the prostate gland. The small glands of Littré

which are present in most parts of the lining membrane of the urethra also contribute to the production of semen.)

The Copulatory Organ. The penis is the intromittent organ of copulation. Besides serving to conduct the urine to the exterior through the channel of the urethra it has the further function of conveying the semen into the genital passages of the female. This latter function is made possible by the power of erection whereby the organ can be inserted into the vagina of the female.

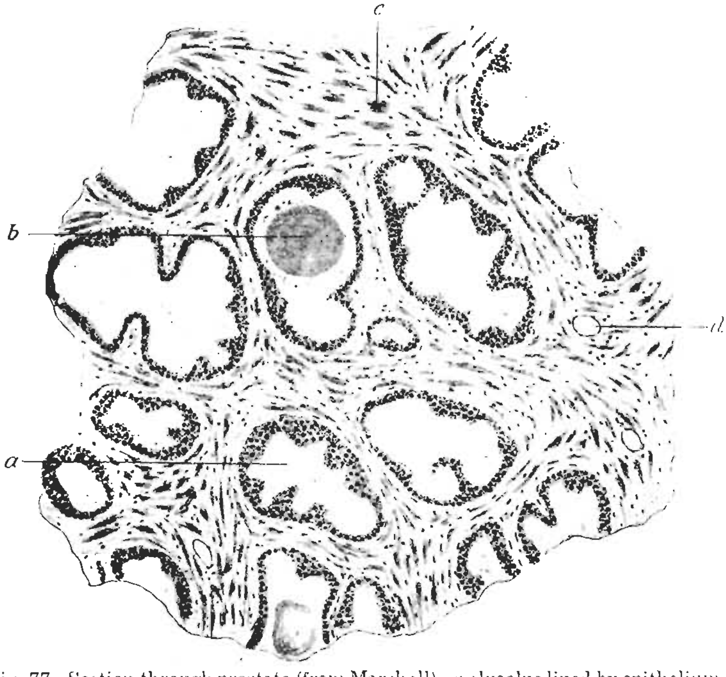


Fig. 77. Section through prostate (from Marshall). *a* alveolus lined by epithelium, *b* concretion (often found in old subjects), *c* muscular fibres amid connective tissue, *d* blood vessel.

The erectile tissue of the penis is contained chiefly in three tracts, the two corpora cavernosa which are situated one on each side and typically are united in the middle line, and the single corpus spongiosum which is placed inferiorly and surrounds the urethral channel. The corpora cavernosa are surrounded by an integument containing connective tissue and unstriated muscle fibres and giving off trabeculae which divide the structures into blood spaces or sinuses. These spaces become engorged with

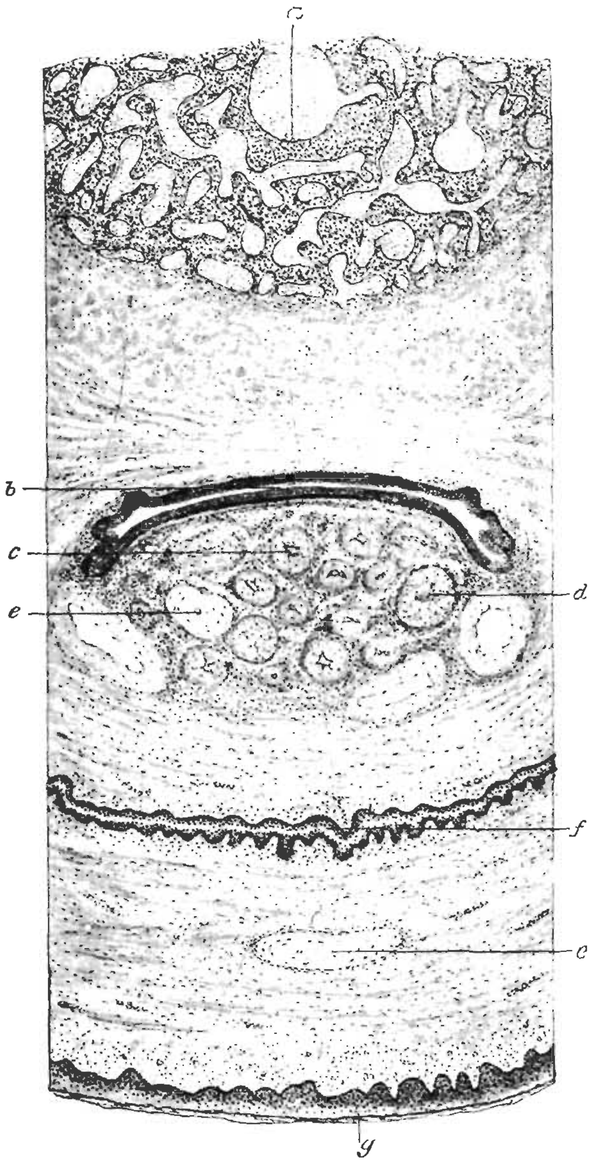


Fig. 78. Transverse section through penis of monkey (from Marshall). *a* erectile tissue, *b* urethra, *c* artery, *d* nerve, *e* sensory end organ, *f* fold of epithelium, *g* surface epithelium.

blood during the process of erection. The corpus spongiosum is similar in structure but its fibrous framework is less well developed. The wall of the urethral canal contains unstriated muscle fibres. At its distal end the spongy body becomes enlarged, forming the glans penis. At their proximal ends all the three bodies are swollen into bulbous enlargements, those of the cavernous bodies being surrounded by the ischio-cavernosus or erector penis muscles, and that of the spongy body by the bulbo-cavernosus muscle. The penis is supplied with blood by the pubic arteries and the dorsal arteries, and the blood is carried away by the dorsal veins and another set of veins communicating with the prostatic plexus. The integument of the penis is a loose fold of skin called the prepuce or foreskin which is especially thick in the bull. Sebaceous glands emitting an odoriferous secretion particularly during rut are present near the free margin of the prepuce. The penis is very sensitive to external stimulation, its surface being beset with numerous Paccinian corpuscles and other sensory end-organs.

The above description applies especially to the human penis, but in the domestic animals the structure of the organ is essentially similar. In the horse the end of the penis (the region of the glans) is

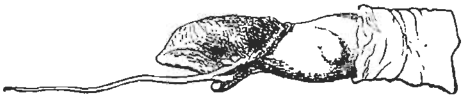


Fig. 79. Penis of ram (from Marshall).

rounded, and when inserted in a state of erection into the vagina of the female occupies the greater part of that passage. In the ram there is a peculiar filiform appendage attached to the left side of the penis, the distal end of which appears to have undergone some sort of torsion. The urethra opens to the exterior at the end of the appendage. This structure, like the main portion of the penis, is composed very largely of erectile tissue which surrounds the urethra and may be regarded as an extension of the corpus spongiosum. Outside of the erectile tissue is a well marked muscular layer which lies next to the integument. The appendage is supported by a pair of fibro-cartilage bodies placed one on each side of the urethra throughout the whole length of the

process. As is shown below there is evidence that the function of the filiform process is insertion into the mouth of the uterus[1].

In the bull the filiform appendage is represented by a vestigial structure or papilla which is situated on the left side of the penis in the same position as the appendage in the ram, only in the bull the process does not project beyond the end of the organ. When erected the bull's penis does not increase in diameter to the same extent as in the horse owing apparently to the thickness of the prepucial folds.

The penis in the boar like that of the horse is not provided with a filiform prolongation or lateral papilla, and the urethral aperture is situated at the end of the organ and in the centre.

Erection, Ejaculation and Coition. The erection of the penis is brought about mainly by the dilatation of its vessels. First of all the proximal portion of the organ increases in size, and then the swelling extends throughout the corpora cavernosa, and eventually to the glans. The arterial pressure in the penis during erection has been found to rise from about one-half to three-fifths of that of the carotid. The erection is effected partly by the contraction of the ischio-cavernosus (or erector penis) and bulbo-cavernosus muscles which arrest the flow of blood along the efferent vessels, but it is believed also that the unstriated muscle fibres which are scattered through the framework of the corpora participate in the process. According to Kölliker the action of these muscles is temporarily inhibited and the trabecular framework of the corpora is correspondingly relaxed. The whole process, which is essentially a reflex action, is presided over by a centre situated in the lumbo-sacral part of the spinal cord, and Eckhard and others have shown that the efferent nerves (called the nervi erigentes) arise from the 1st, 2nd and 3rd sacral nerves and are vaso-dilator in function. On stimulating the nervi erigentes electrically the penis can be made to erect.

Seminal ejaculation is brought about by a series of muscular contractions, which begin in the walls of the vasa efferentia and pass to the epididymis and thence along the vas deferens on either side. The vesiculae seminales contract simultaneously and the prostatic muscles also contract. (The internal generative organs are supplied by nerves coming from the lumbar region, and Langley and Anderson found that stimulation of these nerves in

[1] For description of the uterus and other female organs, see next chapter.

the cat and rabbit produced a powerful contraction of the muscles of the vasa deferentia and related parts. Possibly more than one centre is concerned in the process of ejaculation, but it is evident that the one which presides over the muscular movements of the internal generative organs is situated in the lumbar portion of the cord.

The purpose of penile erection is to give the organ a sufficient rigidity to make it possible to insert the organ into the vagina of the female in the act of coition. In the stallion the erected penis almost fills the vagina of the mare and a considerable amount of friction occurs before seminal ejaculation is completed. In the bull the end of the penis is more or less pointed and it is believed that it is inserted into the mouth of the uterus. In the sheep the filiform appendage is certainly projected into the os uteri. If the appendage is cut off the ram is generally rendered barren. This fact is sometimes taken advantage of by ram traders when wishing to discard tups for breeding purposes. The filiform appendage is removed before the ram is sent to market. Many novices have been deceived by this practice, which is called 'worming'; for such rams are bought by unscrupulous dealers for a butcher's price in open market and then sold at a profit as sound sires.

In the dog the process of coition is different from that of most mammals, and lasts for an unusually long time. This is due to the fact that after the penis has been introduced into the vagina the contraction of a sphincter in the female prevents the withdrawal of the organ until almost fully relaxed.

The friction which is set up between the male and female organs during coition causes a reflex discharge of motor impulses in both sexes, the uterus undergoing a series of peristaltic contractions. Thus Heape has described a sucking action on the part of the uterus in the rabbit, the os uteri dipping down into the seminal fluid at the bottom of the vagina to be withdrawn again in correlation with a rhythmical contraction by the uterine muscles. In the meantime the accessory sexual glands in the female (Bartholini's glands, etc.) emit a secretion which is added to the semen.

Artificial Insemination. This method has been practised with success on mares, cows and other domestic animals in order to overcome certain forms of sterility in the female. It is only

applicable in those species in which ovulation can take place *spontaneously* (that is irrespectively of the occurrence of coition; see p. 183) but this fortunately is the case normally with all farm animals. As Heape has pointed out undue rigidity of the cervix uteri (see p. 166), constriction of the canal, occlusion of the os uteri, or other similar defects may prevent the passage of the spermatozoa into the uterus, while the presence of an abnormal acid secretion in the vagina may kill or deleteriously affect the spermatozoa before they can effect an entry. In such cases the defect may be overcome by inserting the end of a syringe or inseminator into the mouth of the uterus and so injecting the semen directly into the body of that organ. The semen can be obtained either from the vagina of the same mare (or other female animal in suitable cases) or from the vagina of another mare which has just been served, the method being to cause the fluid to collect in a little pocket or depression made by the finger tips and then to draw the semen into the syringe by relaxing the rubber bulb which is held in the hand at the other end of the inseminator and had been previously compressed. In our own experience a not uncommon cause of sterility in mares is evacuation of the semen immediately after service. In such cases the fluid can be caught in a beaker or other vessel on emission from the vagina and then injected. Another method of insemination is to collect the fluid in gelatine capsules which may be placed in the vagina before copulation, and then to remove them after they have been filled, close their lids and insert them into the uterus, either of the same or of another female, when the heat of the body melts the gelatine and sets free the spermatozoa. By this means a number of mares may be impregnated as a result of one service by a stallion.

The possibility of transporting semen from a distance and then utilising it for purposes of insemination is well worthy of consideration, but so far few experiments have been carried out. It has been found however that the spermatozoa of the rabbit retain their vitality within the male generative passages for at least ten days, and that those of other animals can live in suitable artificial media (e.g. glucose and various salt solutions) for two days especially when kept at a temperature sufficiently low to inhibit bacterial multiplication and consequent change in the composition of the fluid.

Castration and the Internal Testicular Secretion. The practice of castration or the removal of the testes has been carried out upon the domestic animals for economic purposes from the earliest times onwards. It is generally believed that the flesh of cattle, sheep, and pigs is much improved thereby, and that the animals fatten faster and more readily, but whether this effect is due directly to the removal of testicular influence upon the metabolism, or whether it is an indirect result of the greater lethargy and absence of excitement displayed by de-sexed animals is still an open question. Castration is practised on horses to make it possible for them to work in association with mares; moreover, geldings are in a general way more manageable and less excitable than entire animals.

It is usual to castrate colts or yearlings in the summer following birth. Calves are operated on at an age of six to twelve weeks. Lambs are castrated at any age between three weeks and three months; and young boars are 'cut' preferably when from six to eight weeks old.

The general effect of castration in all animals is to prevent the development of the secondary male characters, that is, of those characters which while correlated with the sex in question are not directly concerned with the reproductive processes. But this effect is usually only brought about provided that castration is performed prior to puberty or the age when sexual maturity is reached. Thus in man, early castration arrests the enlargement of the larynx and the consequent deepening of the voice; it likewise prevents the growth of hair on the face and the other parts of the body which are usually provided with hair in the adult, and consequently it produces a general appearance of femininity which is in reality a condition in which certain of the male characters are absent rather than one in which female characters have been acquired. In animals the effects are similar. For example, in those breeds of sheep which are horned in the male but hornless in the female (Herdwicks, Merinos, etc.) castration arrests the development of the horns, and it is noteworthy that this happens at whatever stage of growth the operation is performed, the horns ceasing to grow forthwith. It is clear therefore that the testicular stimulus is necessary not only for the initiation of horn growth but also for its continuance. In other breeds of sheep in which both sexes are horned (e.g Dorset Horns, Scottish Black-faced and Lonks) the wethers have horns which are finer and less massive than those of

the uncastrated males and so approximate towards horns of the female type. Early castration in deer prevents the development of the antlers. If the operation is performed late only clump or peruke antlers grow, and these tend to persist instead of falling off in the non-breeding season. If castration is done when the antlers have grown, these fall off, and next season are replaced by peruke antlers. The horn sheath, however, is not shed. In castrated cats the growth of the tissues of the cheek or jowl is partially arrested. In poultry the complete male plumage is not assumed after caponisation or removal of the testes, and the comb, spurs, etc. are said not to develop to their full extent, but there appears to be a good deal of variation in these results.

Another result of early castration in both birds and mammals is the arrest in the ossification of the epiphyses, the consequence being that the limb bones grow larger and that there is a tendency towards giantism such as is associated also with pituitary disease. Again, the thymus gland which normally atrophies at or about puberty persists longer or even hypertrophies in individuals which have undergone castration.

Castration is followed also by atrophy of the prostate and other accessory male glands, or if the operation is carried out before puberty these do not fully develop and sexual desire and penile erection do not occur, not even on stimulating the nervi erigentes artificially.

Transplantation of the testes or of portions of these organs to abnormal positions such as the ventral peritoneum or that of the gut (fowls, etc.) notwithstanding that the ordinary nervous connections of the testes are destroyed, does not arrest the growth of the secondary male characters. It would seem clear therefore that the testicular influence is chemical and not nervous, that is to say, that it acts by the internal secretion of substances into the blood, and that these substances are carried in the circulation to the various tissues influenced by them, growth and seasonal activity being thus brought about.

The further question arises as to what part of the testis is concerned in elaborating this internal secretion or hormone. It has already been mentioned that in those animals in which testicular transplantation to abnormal positions had been carried out castration effects did not occur, and this is also true for animals in which the vasa deferentia had been cut. In such experiments, however,

the spermatogenetic tissue underwent degeneration owing to the semen being unable to escape. The same effect is brought about by exposing the testes to the influence of Röntgen rays, as has been shown more especially by experiments on roe-deer by Tandler and Gross. On the other hand, the interstitial cells of the testis were not affected in any of these experiments, and the development of the secondary sexual characters (growth of horns, etc.) must be correlated with the persistence and functional activity of these cells. It must be concluded therefore that the interstitial cells are responsible for the secretion of the testicular hormone.

Further experiments have shown that unilateral castration in Herdwick rams does not affect the symmetry of horn growth, while, according to Ribbert, there is evidence that removal of one testis may be followed by compensatory hypertrophy on the part of the other.

CHAPTER XIII

THE FEMALE GENERATIVE ORGANS AND THE MAMMARY GLANDS

The Ovaries are a pair of organs lying in the abdominal cavity to whose dorsal wall they are connected by the broad ligament which stretches across the body wall in this region. They are composed of a stroma or ground substance of connective tissue containing blood vessels and a number of vesicles of varying

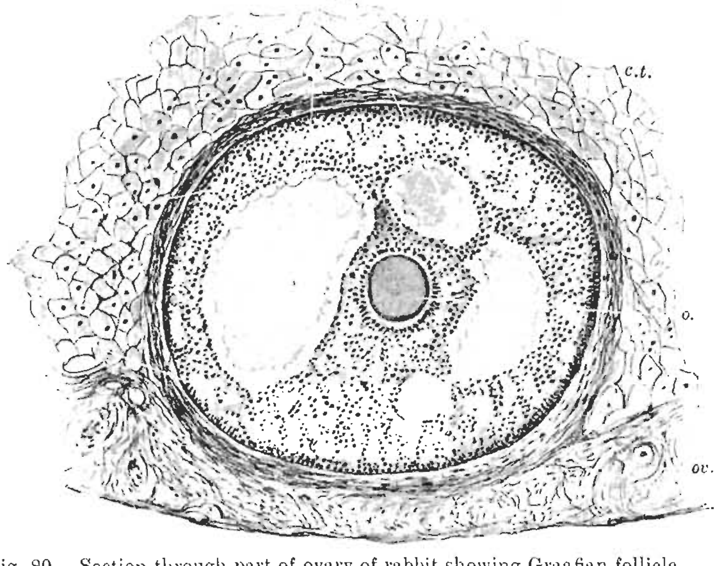


Fig. 80. Section through part of ovary of rabbit showing Graafian follicle (from Marshall). *c.t.* connective tissue wall of follicle, *f.e.* follicular epithelium, *l.f.* liquor folliculi, *o.* ovum, *ov.* primordial ovum.

sizes called the Graafian follicles. The smallest of these—the primordial follicles—however, have no cavity, but consist merely of ova surrounded by a single row of epithelial cells; they lie just below the surface of the ovary. As the follicles increase in size they pass inwards towards the centre of the stroma, the epithelial

cells multiply and a space is formed between those immediately covering the ova and the outer cells which are contiguous with the modified connective tissue which forms the outer wall of the follicle. This space is filled with a fluid containing protein substances, etc., the liquor folliculi, which is concerned in the nourishment of the ovum. The two portions of follicular epithelium, each of which is several cells deep, are connected by strands of similar cells. Each follicle contains one ovum (rarely two or more) and the largest or most mature follicles may occupy a considerable part of a section through an ovary; they may protrude visibly from the surface of that organ and in some animals (sow, etc.), at the approach of the 'heat' periods, the ovary presents almost the appearance of a bunch of small grapes. In addition to follicles the ovaries at certain seasons contain yellow pigmented bodies, or corpora lutea. These, as will be described presently, are formed from the ruptured follicles after the discharge of the ova. Epithelioid interstitial cells are also generally present in the stroma.

The Fallopian Tubes or **Oviducts** whose function is to convey the discharged ova to the interior of the uterus open internally into the body cavity close to each ovary. The ova pass into the fimbriated expansions at the ends of the tubes, which are provided with cilia to direct the passage of the ova. Internally the oviducts are lined by a ciliated epithelium outside of which are connective tissue and muscle. It is believed that the fimbriated ends of the tubes erect at each ovulation In some animals (dog, ferret) the ovaries are enclosed by a membranous covering which is continuous with the wall of the tubes, so as to ensure the discharged ova passing into the tubes and not being lost in the body cavity[1].

The Uterus. The tubes which are attached to the broad ligament (or fold of peritoneum which connects the ovaries and uterus with the body wall) become expanded, passing backwards into the horns of the *uterus* (*cornua uteri*). These in many animals (mare, cow, ewe, sow, etc.) unite to form the body of the uterus (*corpus uteri*) which opens into the *vagina* or common urogenital passage of the female. The posterior end of the uterus is narrowed down to form the cervix, the actual uterine opening being called the *os uteri*. In the rabbit the uterine horns open separately but close together in the vagina. In man the uterine horns are so much

[1] Vestigial structures called the parovarium and paroöphoron are found in some animals between the ovary and tube.

reduced as to be almost unrepresented, the oviducts only expanding slightly for a short distance before opening into the body of the uterus.

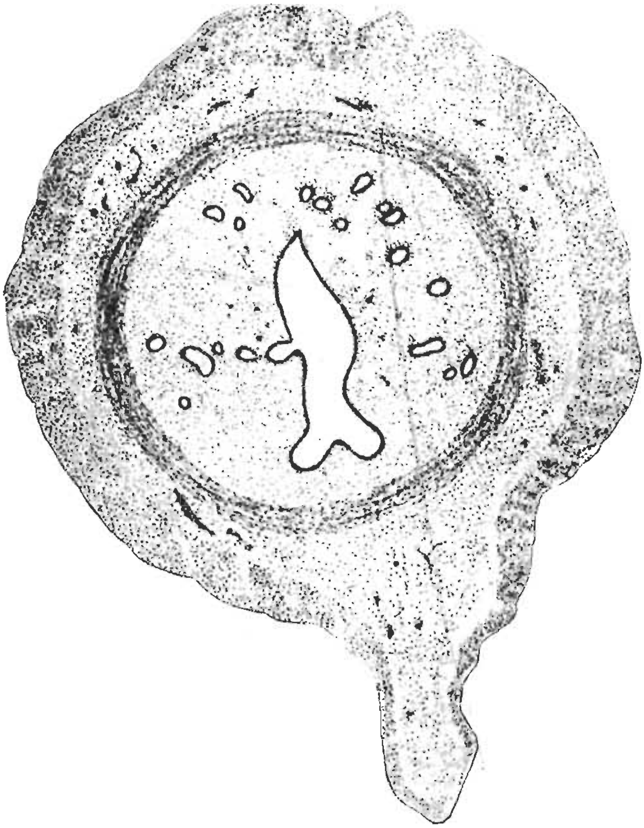


Fig. 81. Transverse section through uterine cornu of rat (from Marshall).

The cavity of the uterus is lined by a ciliated cubical or columnar epithelium which together with the stroma beneath composes the uterine mucosa. This contains glands which open into the cavity and have a secretory epithelium continuous with and similar to the epithelium bounding the cavity. The glands are sometimes very numerous, and vary in activity at different periods. The stroma is a primitive kind of connective tissue and contains vessels which increase in size and number at the approach of 'heat' as will be described later. The stroma is

surrounded by unstriated muscular tissue which is arranged in two (or three) layers, the inner layer consisting of circular and the outer of longitudinal fibres. Connective tissue with good sized vessels is also present in the muscular layers. Outside of all is *the serous or peritoneal coat.*

The Vagina into which the male organ penetrates during coitus extends from the uterus to the exterior opening. Its walls contain

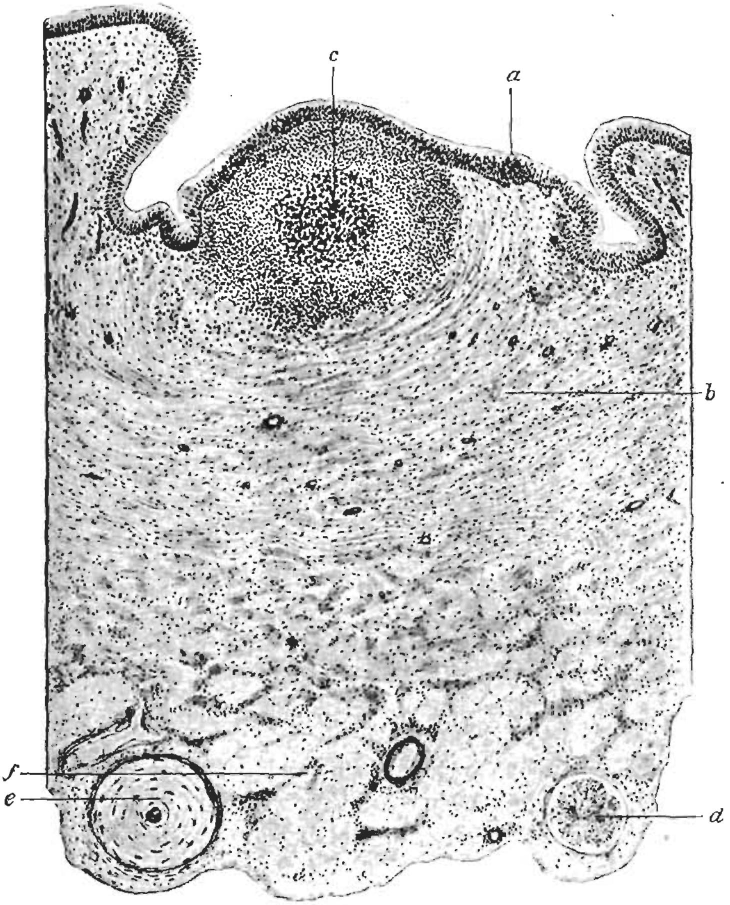


Fig. 82. Section through vagina of monkey (from Marshall). *a* epithelium, *b* sub-mucous layer, *c* lymphatic gland, *d* nerve, *e* sensory end-organ, *f* fat cells.

longitudinal and circular muscle fibres, and internally it is lined by a stratified scaly epithelium. The female generative organs

which are visible externally are known collectively as the vulva. The clitoris is a small rod-like organ and represents the penis of the male, but unlike the latter is solid.

The Mammary Glands, the function of which is to provide a nutritive secretion for the newly born young, though rudimentary in the male are normally active only in the female. Their numbers and position vary in different species. (In animals which possess a number of mammary glands, as with the pig, these are usually arranged in rows approximately parallel on the ventral side of the thorax and abdomen. In the cow the mammae are contained within a definite milk-bag or *udder* which is surrounded by a fibrous envelope and suspended below the abdomen.) This udder is provided with milk cisterns or galactophorous sinuses into which the ducts of the glands open and convey milk from the secretory alveoli. Each sinus communicates with the exterior by a teat, there being typically four teats in a cow, corresponding to the four mammary glands (and sinuses), commonly called the four 'quarters.' One quarter may run dry without the others but this does not happen normally. There is a fibrous division consisting of yellow elastic tissue between the two lateral halves of the cow's udder, but not between the anterior and posterior parts. Very frequently there are one, two, or even three extra teats which are placed posteriorly to or between the other teats, but are usually smaller than the normal; these supernumerary teats are associated with extra glands from which the milk constituents may be re-absorbed into the blood (the milk sugar sometimes appearing in the urine) since the secretion is not usually drawn off through the teats.) In the sheep there are normally only two glands, sinuses and teats (occasionally four), and the mare is similar excepting that there may be two or even four sinuses opening into one teat.

The actual glandular tissue is divided into lobes, which are sub-divided into lobules, containing secretory alveoli. These are bound together by connective tissue. The ducts through which the milk passes have walls containing alveolar tissue and some unstriated muscle fibres, and are lined internally by columnar epithelial cells. In the secretory cells of the alveoli an active and a resting stage can be distinguished. In the latter the lumina are wide, and the cells of the lining epithelium form a single flat layer with centrally situated nuclei. In the active condition the epithelial cells are long and columnar and project into the cavity.

In these cells granules (containing a protein material) and fat globules accumulate, and afterwards form the milk constituents which the cells discharge into the lumina of the alveoli. The so-called 'colostrum corpuscles' which occur in the milk in the first few days after parturition or shortly before are probably white corpuscles since they have been observed to undergo amoeboid movement.) The milk constituents which are formed during lactation are discharged into the lumina of the alveoli without the cells which excrete them becoming detached or destroyed in the

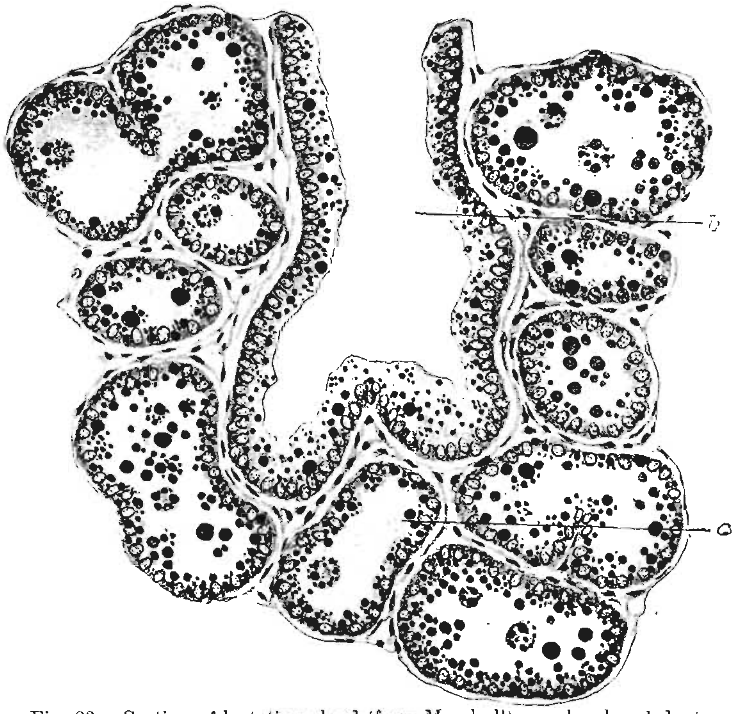


Fig. 83. Section of lactating gland (from Marshall). *a* alveolus, *b* duct.

process. The milk thus produced passes from the alveoli into the ducts and sinuses whence it is drawn off by the teat being sucked. (In the pig the tissue lining the ducts of the mammary glands may contain black or coloured pigment. This is clearly related to the pigment of the hair, since it is only present in the coloured breeds of pigs. It occurs in both normal and spayed sows, and occasionally also in the hog in which rudimentary

mammary glands (or at any rate ducts) may be found. When present in some quantity, as frequently happens, it gives rise to the condition known as 'seedy-cut,' a term which implies that the bacon of the 'belly-piece' is discoloured. The pigment however is perfectly harmless, and unlike the black pigment in the uterus of the ewe (described below) is not blood pigment.)

The season of the year when an animal of any species or variety undergoes sexual intercourse has been called by Heape the *sexual season* for that animal. The actual periods at which copulation occurs are the oestrous periods. These may recur at rhythmical intervals within one sexual season as with the mare, the cow, the ewe and the sow (polyoestrous animals in Heape's terminology), or there may be only one oestrus to the sexual season as with the bitch (monoestrous animals).

A simple oestrous cycle in an animal of the latter kind (e.g. the bitch) has been divided into a number of periods as follows:

Anoestrum[1] (period of rest),
Prooestrum[1] (period of growth and congestion and period of destruction),
Oestrus (period of desire),

Pregnancy Pseudo-pregnancy.

The complete cycle in the monoestrous dog lasts about six months, there being two sexual seasons and 'heat' periods in one year, these occurring typically in spring and autumn, but there is some individual variation. In the smaller kinds of dogs the duration of the cycle may be less than six months while in the larger varieties it may extend over a longer time.

The *anoestrum* in the absence of pregnancy lasts for about five months. The generative organs are in a state of quiescence. The ovarian follicles are probably undergoing a slow process of growth and ripening throughout the anoestrum, but they are not conspicuous upon the surface of the organs, at any rate until the approach of a new heat period. It follows that ovulation does not occur during the anoestrum and the ovaries do not contain corpora lutea. The uterus is relatively anaemic and the glands inactive. The mammary glands also are in a condition of rest unless lactation is going on as a result of recent pregnancy.

[1] These terms were given by Heape to the periods as above described.

The *prooestrum* which is the period of 'coming on heat' is marked by increased activity on the part of all the generative organs. The Graafian follicles which at any earlier stage were situated more centrally within the ovary, increase in size so as to become easily visible on the surface from which they may protrude. The prooestrous uterine changes may be divided into two stages: (1) growth and congestion, and (2) destruction. In the first stage the uterine mucous membrane becomes thicker and more extensively vascularised, the capillaries being increased both in size

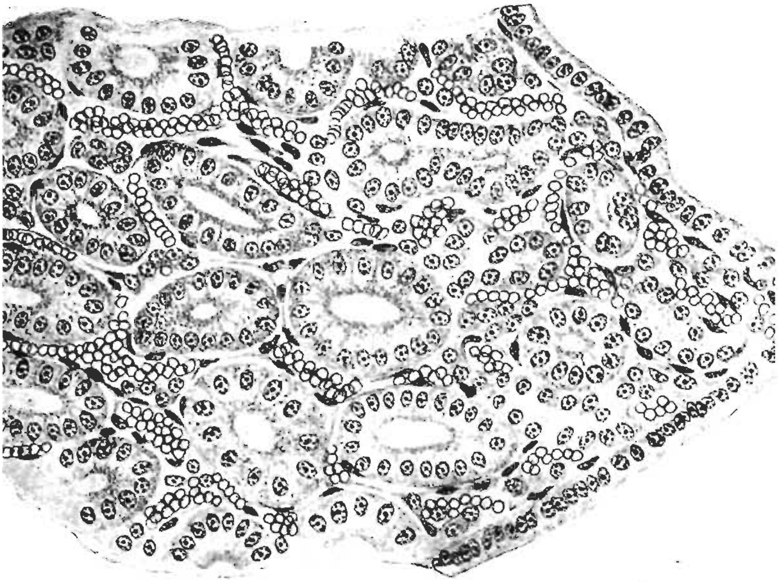


Fig. 84. Section through prooestrous uterine mucous membrane of dog showing congested blood vessels between the glands (from Marshall).

and number and the glands becoming more active. In the second stage the walls of a certain number of capillaries break down and the blood corpuscles are extravasated in the stroma, and tend to become congregated just below the uterine epithelium; the latter ruptures in certain places and blood is poured out into the cavity of the uterus whence it passes down to the vagina and to the exterior. Bleeding from the external vaginal opening in the prooestrous bitch may last for a week or even longer, and the entire prooestrum lasts for from ten to fourteen days. The whole process must be regarded as an act of preparation on the part of

the uterus for the reception of a fertilised ovum, for at this period the superficial tissues of the mucous membrane undergo a process of partial renewal. The prooestrum corresponds to menstruation in women, but its manifestations are less pronounced.

Oestrus is the period of desire and sexual intercourse is ordinarily restricted to this period. In the bitch it lasts for about a week. Ovulation or the rupture of the Graafian follicles and the discharge of the ova occurs during this period. The final maturation of the ova commences just prior to ovulation and is completed in the Fallopian tube. The process is similar to that

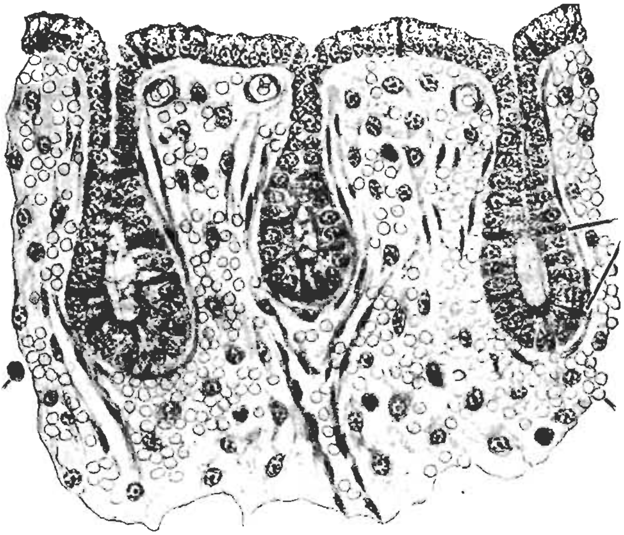


Fig. 85. Section through prooestrous uterine mucous membrane of dog showing extravasated blood (ex. b.), pol. polymorph leucocyte, sec. cells showing secretory activity (from Marshall).

which occurs in spermatogenesis (see p. 153) and results in the nuclear material of the mature ovum being reduced to one half of what it was previously, that is to say, the number of chromosomes is one half that of the normal number which is characteristic of the cells of the body for the species in question (in the horse 26, and in man 24).

The maturation of the ovum differs from the corresponding process in the spermatozoon in the unequal division of the cell. In the first division (which is the reduction division, the chromosomes not splitting longitudinally as they do in all other cell divisions) the first polar body is extruded. This consists of half the nuclear

material. The second division results in the formation of the mature *ovum and the second polar* body (the latter consisting like the first polar of nuclear material). The two polar bodies are extruded when the ovum is in the tube; sometimes the first polar body divides into two equal halves so that altogether there are three polar bodies; all of these die and disappear, the mature ovum with the reduced number of chromosomes alone remaining. The normal number is restored by the union with a spermatozoon, this process usually occurring in the Fallopian tube.

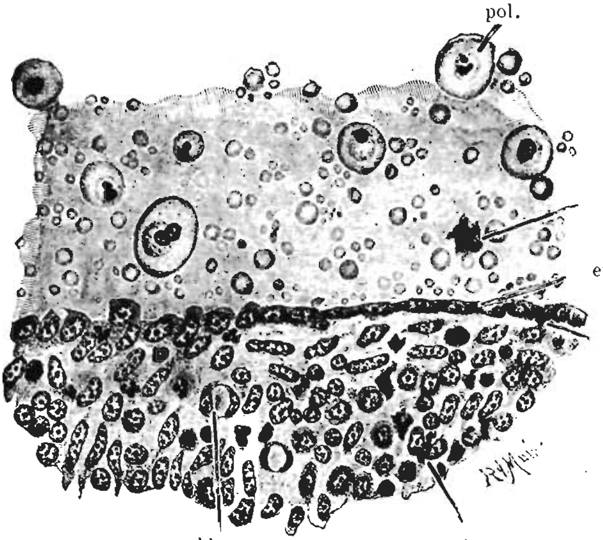


Fig. 86. Section through edge of mucous membrane of dog during early recuperation (from Marshall). bl. v. blood vessel, ep. epithelium in process of renewal, pig. pigment, pol. polymorph leucocyte.

During oestrus the mucous membrane of the uterus becomes recuperated and external bleeding from the vaginal opening ceases.

Oestrus in the bitch is followed either by pregnancy or by pseudo-pregnancy according to whether or not the ovum or ova become fertilised as a consequence of coitus. Under both conditions the uterus undergoes *growth changes which relate chiefly* to the blood vessels and glands in the mucosa. These increase in size, the whole organ assuming a histological appearance indicative of great activity. The secretion coming from the glands is a

source of nutriment to the foetus in pregnancy and in some animals has been designated uterine milk; in pseudo-pregnancy a fluid is similarly secreted and as if intended for a foetus. Decidua cells (that is to say, modified stroma cells the development of which is correlated with the development of the foetal membranes and the nourishment of the unborn young) are not found normally except in the presence of an embryo. Apart however from this difference the changes undergone by the uterus of the bitch during pseudo-pregnancy are in a general

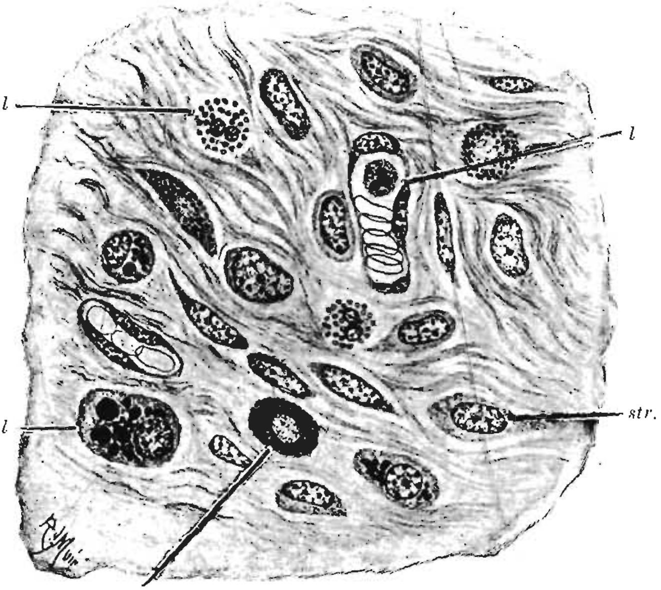


Fig. 87. Section through portion of uterine mucous membrane of dog during early recuperation showing different kinds of leucocytes (*l.*) (from Marshall). *str.* stroma cell.

way similar to those which take place in true pregnancy, but are less pronounced. The growth changes of pseudo-pregnancy are succeeded after about four or five weeks by degenerative changes when the glands become shrunken and blood is extravasated into the tissue, but without leading to external bleeding. A somewhat similar condition occurs in the last stage of pregnancy.

The ovarian changes also are identical under the two conditions, at any rate, in the earlier stages. At ovulation the egg along with some of the follicular epithelial cells and most of the

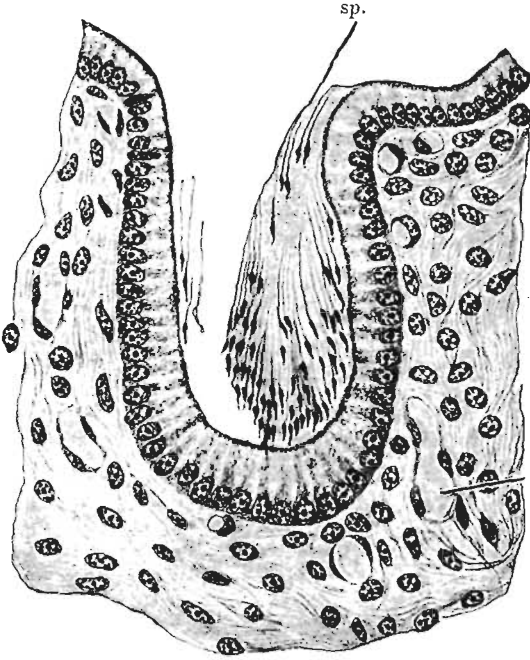


Fig. 88. Section through uterine gland of bitch after coition showing spermatozoa (sp.) (from Marshall). bl. v. blood vessel.

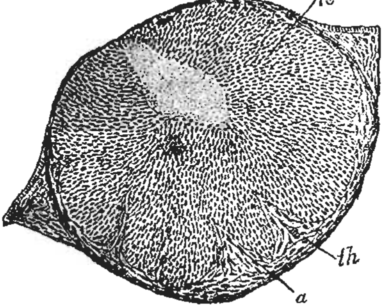


Fig. 89. Recently ruptured follicle of *mouse (after Sobotta from Schafer). fe* follicular epithelium, *th* connective tissue, *a* ingrowth from same.

liquor folliculi is discharged from the ovary. The remaining epithelial cells then undergo a great and rapid hypertrophy becoming *converted into the luteal cells of the fully formed corpus luteum.* At the same time strands of connective tissue grow inward from

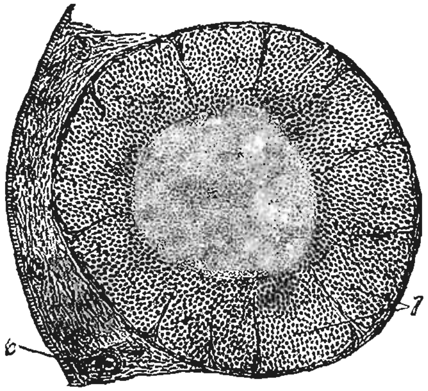


Fig. 90. Early stage in formation of corpus luteum of mouse (after Sobotta from Schafer). *l* developing luteal cells, *g* germinal epithelium.

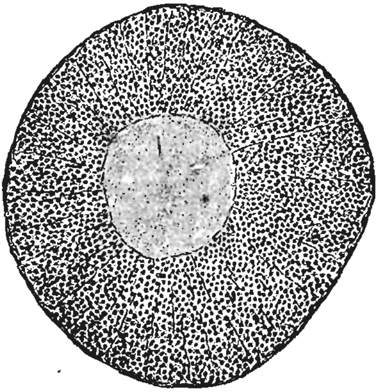


Fig. 91. Late stage in formation of corpus luteum of mouse (after Sobotta from Schafer).

the wall of the follicle carrying blood vessels along with them, so that the completely developed corpus luteum consists of large luteal cells partly separated by an anastomosis of connective tissue, the whole structure being highly vascularised. The remains of the central cavity of the original follicle is eventually filled in by a plug of connective tissue. The epithelial cells increase to

about sixteen times their original cubical content and come to contain a yellow pigmented fat called lutein. The corpus luteum thus formed persists in the dog until the close of pseudo-pregnancy or pregnancy when the luteal cells become vacuolated and shrink. The corpus luteum eventually degenerates, leaving merely a scar.

Contemporaneously with the growth of the corpus luteum the mammary glands develop both during pregnancy and during pseudo-pregnancy, and milk secretion may occur at the end of

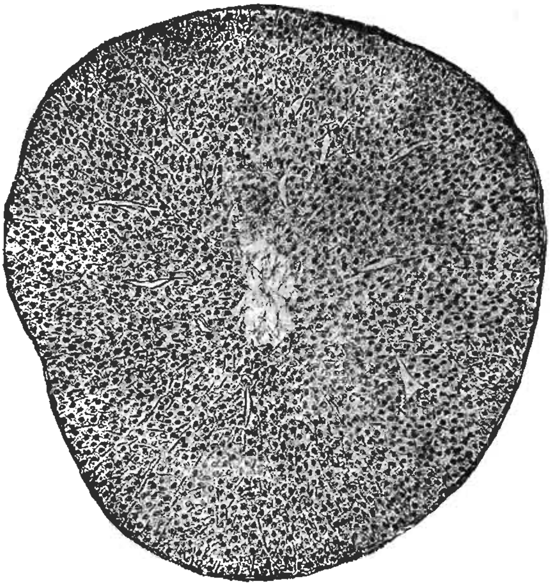


Fig. 92. Fully formed corpus luteum of mouse (after Sabotta from Schafer).

each of these periods but the growth of the glands and their subsequent activity are less incomplete when true gestation does not take place.

The period of gestation in the dog is about 62 days, and pseudo-pregnancy may be said to last for about the same time or perhaps not quite so long. It does not terminate so abruptly as true pregnancy, and the uterus passes gradually back to the condition of quiescence which is characteristic of the anoestrum[1]. This

[1] It is noteworthy that at the end of pseudo-pregnancy a bitch may behave like one about to give birth and prepare a bed for pups. Hammond has noted similar phenomena with doe rabbits which (exceptionally) experience pseudo-pregnancy.

period lasts for about three months and is succeeded by another prooestrum.

Polyoestrous animals differ from monoestrous ones in having short recurrent cycles within a single sexual season. Thus in the sheep the 'tupping time' may take place in autumn, and during this season the ewe will experience a succession of cycles, each lasting about 15 days, until pregnancy is induced or tupping is over; in the latter case the ewe passes into a state of prolonged sexual quiescence (anoestrum) which lasts until the next tupping season in the following autumn. The return of oestrus at short intervals during the sexual season is implied when the shepherds speak of the ewe as 'coming back' to the ram.

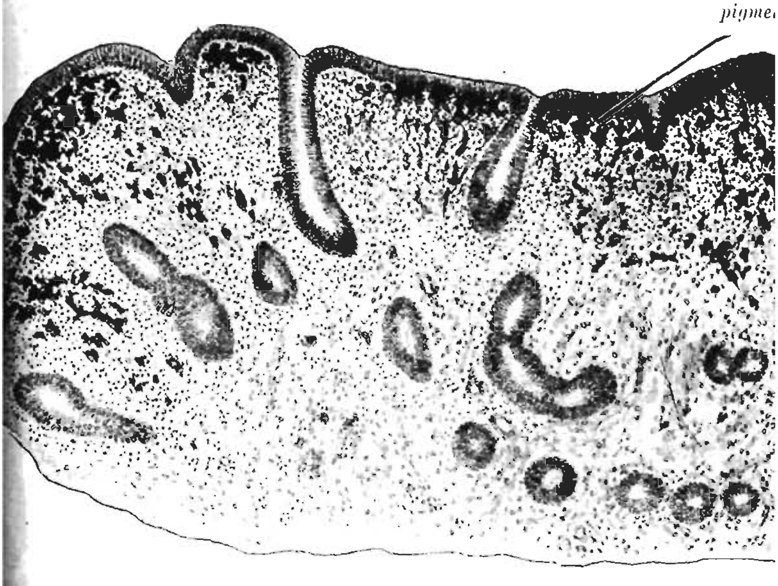


Fig. 93. Section through uterine mucous membrane of sheep shewing pigment formed from extravasated blood (from Marshall).

The short interval of rest between the 'heat' periods is called by Heape the dioestrum and is characteristic of all polyoestrous animals. In the sheep it lasts for about 12 or 13 days. It is followed by a brief prooestrum when the ewe's external generative organs become somewhat congested. There is however no external bleeding in the ewe, and the uterine blood which becomes extravasated during the prooestrum remains in the stroma, coming to lie just below the epithelium where it is converted into black

pigment. After three or four heat periods this pigment may have accumulated in such quantity that almost the whole surface of the uterine mucosa is rendered jet black, the pigment only disappearing during subsequent pregnancy or during the anoestrum when it is said to be removed by leucocytes.

Oestrus in the ewe may last for a day or for only a few hours, and the prooestrum and oestrus together do not occupy more than two or three days. Ovulation takes place during oestrus and the number of follicles which discharge is usually one or two, sometimes three, but rarely more than three.

The wild sheep (such as the Mouflon or the Barbary sheep) is said to be monoestrous and to experience only one sexual season annually. The Scottish Black-faced sheep in the Highlands is generally dioestrous, that is to say, it can have two 'heat' periods in the absence of the ram but not more than two, and the season for tupping is November. In the Lowlands, however, where the climate is less severe and food more abundant, there may be five or six dioestrous cycles if the ewe fails to become pregnant before anoestrum or prolonged quiescence is resumed. Amongst the English breeds the number of recurrent 'heat' periods is generally much greater and in Dorset Horns and Hampshire Downs the ewes may experience oestrus at almost any time of the year. The same is true of the Merino sheep amid favourable conditions, and in New South Wales the sexual season is said to embrace the whole year, there being in the absence of pregnancy an almost uninterrupted succession of dioestrous cycles. Amongst English varieties the Dorset Horns are almost alone in being able to have two crops of lambs in one year, but this practice is discouraged as it tends to cause too great a strain and thus deteriorate the ewe. The capacity to experience oestrus or the degree of polyoestrum is partly a racial characteristic, but it depends at least equally upon environment and nutrition which favour an increased fecundity.

The period of gestation in the sheep is 21 to 22 weeks or about five months, so that if lambing occurs twice in one year there is only about a month's interval between the end of one pregnancy and the beginning of the next.

The corpus luteum, which as we have seen is formed from the discharged follicle, develops very rapidly in the sheep. Its fate depends upon whether or not gestation supervenes as a result of coitus, for in the pregnant animal the corpus luteum goes on in-

creasing in size until about half way through the period and maintains its functional activity till at or near the time of parturition, whereas in the non-pregnant ewe after oestrus the organ continues to develop for only a few days before it becomes smaller. Mature (or almost mature) Graafian follicles are not associated with corpora lutea, and the latter organs when present appear to exercise a dominating influence upon the ovarian metabolism and to inhibit follicular growth or even to promote follicular atrophy. Consequently it is important in animals which come 'on heat' at short intervals that the corpus luteum should not persist for more than a short period, and this suppression of the corpus luteum in the non-occurrence of pregnancy is generally characteristic of polyoestrous mammals. In monoestrous animals between the heat periods and in all animals under a condition of pregnancy it is obviously not disadvantageous if ovulation or the ripening of the Graafian follicles is partially inhibited during these times when coitus does not occur. Correlated with the shortening in the period during which the corpus luteum persists (i.e. in polyoestrous animals) there is no pseudo-pregnant development of the uterus and mammary glands. Even in polyoestrous animals, however, the corpus luteum may abnormally persist and cause sterility, and Williams recommends that when this happens with cows the corpus luteum should be squeezed out from the ovary, and states that when this is done the oestrous cycle starts again forthwith, the cows very soon coming 'in use' after the operation of removal.

The cow like the sheep is polyoestrous, but the dioestrous cycle lasts for 21 days. The precise conditions which determine the duration of the sexual season are little understood, and investigation into this subject is urgently needed with the view of controlling the bulling times of heifers and cows so as to regulate the periods of calving and the supply of milk throughout the year. The prooestrous changes like those of the ewe are relatively slight and external bleeding from the vaginal opening does not usually occur. There is sometimes a mucous discharge but even this may be absent, and yet a normal oestrus may supervene. Owing to this circumstance some 'cowmen' will let a 'period' pass by, and so lose three weeks, and possibly the chance of getting an animal in calf for that season, simply because they failed to detect any of the signs of the onset of 'heat.' Dioestrous cycles (in the non-

occurrence of pregnancy) may continue for half the year or even longer but there is much individual variation. The period of gestation is nine months. Usually only one follicle is discharged at oestrus. Heat may supervene six weeks after parturition. Pro-oestrum and oestrus together only occupy two or three days.

In the sow the dioestrous cycle is also three weeks and pregnancy lasts four months. By weaning the young pigs early and giving the sow a plentiful supply of food it is possible to obtain five litters in two years, but the more usual practice is to have two litters annually. Heat may be experienced four weeks after farrowing and in the absence of the boar continue to recur at intervals of three weeks, each oestrous period lasting about a day. The indications of prooestrum are slight, there being generally no external bleeding, but the vulva is swollen.

In all the above-mentioned animals oestrus is a period of restlessness and excitement. The ewe on heat tends to follow the ram. The cow or heifer bellows and mounts other cows, and sometimes there is a slight rise of body temperature. The sow emits a peculiar grunting sound which is characteristic of oestrus and is not made at other times. But as compared with the bitch the symptoms of oestrus are slight and of brief duration.

The mare is polyoestrous, the normal dioestrous cycle being about three weeks and the oestrous period four or five days, though its actual length may vary by three or four days. The sexual season in the absence of the stallion extends throughout the spring and early summer months, and is generally longest in the more domesticated breeds. Ewart has recorded a case of a pony imported from Timor (which is in the Southern Hemisphere), to Scotland, in which oestrus was experienced in the autumn, or at the same time as the spring in Timor. The period of gestation in the mare is eleven months, and 'heat' recurs from nine to eleven days after parturition. This is called the 'foal heat.' Certain mares are irregular in the recurrence of the 'heat' periods, and, in some, 'foal heat' does not occur until seventeen days after parturition instead of the usual time. In exceptional cases a mare, like a cow, may conceive at the 'foal heat' and yet take the horse three weeks later, just as though she had failed to become pregnant. Heape states that, very exceptionally, mares are monoestrous. Blood has been observed in the mare's prooestrous discharge, but it is not generally present. The external generative organs,

however, are usually swollen and mucus is emitted. The clitoris and vulva often undergo a succession of spasmodic movements, preceded by the discharge of small quantities of urine and this fluid may have the consistency of oil. Suckling mares tend to fail in their milk supply, and the quality of the milk appears to undergo some kind of change, as it is frequently found that foals during the heat periods of their dams suffer from relaxation of the bowels or even acute diarrhoea. In mares which are not suckling the mammary gland becomes congested and increases in size during the heat. At the same time some mares develop great excitability, and kick and squeal, becoming dangerous to approach and impossible to drive. There is, however, great variation, for other animals may pass through the 'heat' period without exhibiting any well-marked signs of their condition which in a few instances can only be determined by the behaviour of the mare towards the stallion.

Of other domestic animals the cat is polyoestrous and has a dioestrous cycle of about 14 days and three sexual seasons annually, and the period of gestation is nine weeks. The ferret is monoestrous and has two or three sexual seasons which are however usually confined to spring and summer. Gestation lasts 40 days. The rabbit and other wild rodents are polyoestrous.

In the mare, cow, ewe, sow and bitch ovulation takes place spontaneously, but in the cat, rabbit and ferret it requires the additional stimulus set up by coitus before it can occur. Presumably coitus causes a nerve reflex. In the rabbit ovulation takes place from 9½ to 10 hours after coitus. Maturation of the ovum also depends upon the occurrence of coitus and commences shortly afterwards, but is not completed until after ovulation. In such animals as the rabbit which do not ovulate spontaneously, corpora lutea are not usually formed apart from pregnancy, and the pseudo-pregnant condition does not normally occur.

Pregnancy. The ova are fertilised by the spermatozoa in the Fallopian tube. A spermatozoon after coming in contact with an ovum passes bodily through its wall, the head or nucleus of the spermatozoon fuses with the nucleus of the ovum, thus restoring the amount of nuclear material or number of chromosomes to that characteristic of the species, while the tail of the spermatozoon breaks up and mingles with the external (or non-nuclear) protoplasm of the ovum. The fertilised ova then pass down the

tube and into the uterine cavity. Here they find a rich pabulum of nourishment provided by the prooestrous discharge. After a few days each ovum sinks down into the uterine mucous membrane (which in man grows round it forming the decidua reflexa. In the mare up to the seventh week the young is nourished by the yolk sac which opens widely into the embryonic gut and is also the means of attachment of the young to the uterine wall. The ovum meanwhile has undergone segmentation and become converted into the embryo, and the embryonic or foetal membranes grow outwards and form a bag containing a watery fluid. The outer of these membranes is called the chorion and gives off

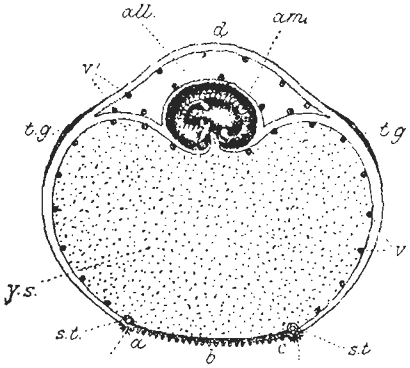


Fig. 94. Diagrammatic representation of 4 weeks' horse embryo and its foetal appendages (after Ewart from Smith, Messrs Baillière, Tindall and Cox). *am.* amnion, *y.s.* yolk sac, *st.* and *v.* blood vessels, *d.* chorion, *t.g.* area of special attachment to uterine wall, *all.* allantoic cavity, *a.b.c.* absorbing area of yolk sac.

villi which project as finger-like processes into spaces in the maternal tissue of the uterus. The attachment by the yolk sac is then replaced by the attachment through the chorion. Meanwhile the uterus of the mother undergoes great changes, its muscle walls becoming enormously developed, while the outer portion of the connective tissue of the stroma gives rise to spindle-shaped decidual cells and at the same time becomes very greatly vascularised. This tissue forms the maternal placenta and contains large blood sinuses into some of which the chorionic villi project. In the meanwhile from a point within the embryo an outgrowth called the allantois arises, and the outer wall of

this outgrowth blends with the chorion to form the foetal placenta. The portion of the allantois remaining within the foetus eventually becomes the bladder, and the point from which the allantois passes out remains after birth as the navel. The chorionic villi contain blood vessels connected with the circulatory system of the developing foetus so that the foetal and maternal circulation are brought into very intimate relation, being only separated by a very thin wall of protoplasm, but there is no direct communication between them. Nutritive material—protein, fat and carbohydrate as well as oxygen—transfuse through this thin layer, from the mother to the young, while excretory products and carbon

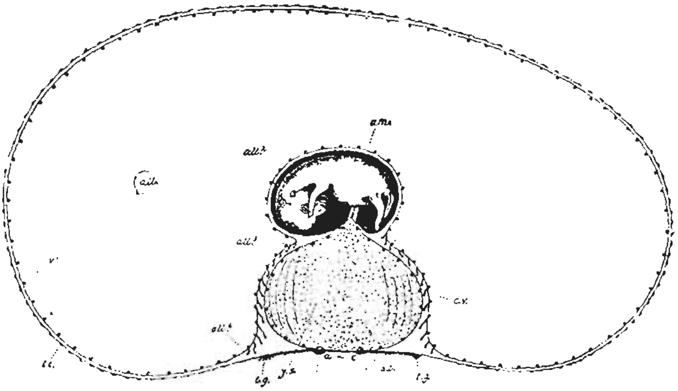


Fig. 95. Seven weeks' horse embryo (after Ewart from Smith, Messrs Baillière, Tindall and Cox). *all.* allantoic cavity, *am.* amnion, *c.v.* villous process between allantois and yolk sac, *y.s.* yolk sac, *v′* and *tt′* vascular villi, *a*—c absorbing area of yolk sac, *t.g.* area of special attachment.

dioxide pass in the opposite direction from the foetal to the maternal circulation. In this way the placenta acts as a foetal alimentary canal, lung and kidney, but there is never any actual contact between the maternal and foetal blood. In later embryonic life the foetus retains its connection with the chorion and so with the maternal placenta, by the umbilical cord which is formed partly from the allantois, and contains the umbilical arteries and vein.

The form and mode of attachment of the placenta are different in the various orders of mammals. The chorionic villi may be so interlocked with the maternal tissue that in parturition some of the uterine mucosa is torn away from the remainder leaving a raw surface. This is what happens in man and in the dog as well as

in many other mammals. In the horse and other Ungulata, however, this does not happen. In the Carnivora the villi are confined to a zone or belt, in ruminants they occur in clumps or cotyledons corresponding to the cotyledonary papillae which in these animals protrude from the uterine mucous membrane, while in the horse and pig the villi are scattered.

The highly developed uterine glands supply a secretion (called

Fig. 96. Foetal circulation, advanced period (*after* Colin, *from* Fleming, Messrs Bailliere, Tindall and Cox). *A* cotyledons, *B* umbilical vein which communicates with *C* and *D*, venae portae (in liver) and with ductus venosus (opening into *F*, posterior vena cava, *G* right venticle, *H* pulmonary artery, *I* ductus anteriosus (uniting *H* and *J*), *J* aorta, *L* umbilical arteries.

in ruminants the *uterine milk*) which helps to nourish the developing foetus.

The beginning of gestation is marked by a change in the character of the mother. The pregnant cow and sheep 'settle' or tend to fatten in the early months, and graziers take advantage of this fact to get the animals into good condition for market. Mares which were previously troublesome and difficult to work

become quiet and tractable. The abdomen becomes visibly enlarged as may be most easily seen from behind and undergoes an alteration in shape, the flanks tending to become hollow, while the belly sinks. These changes in the mare are noticeable after about four months. In the meanwhile the foetus is developing in the uterus, and by the end of the fourth month may be seen to respond to stimuli; thus a bucket of cold water given to the mother on an empty stomach will cause the young foal to make a sudden twitching movement which can be seen externally on the left side of the mare. The enlargement of the mammary glands may be seen most easily in animals pregnant for the first time.

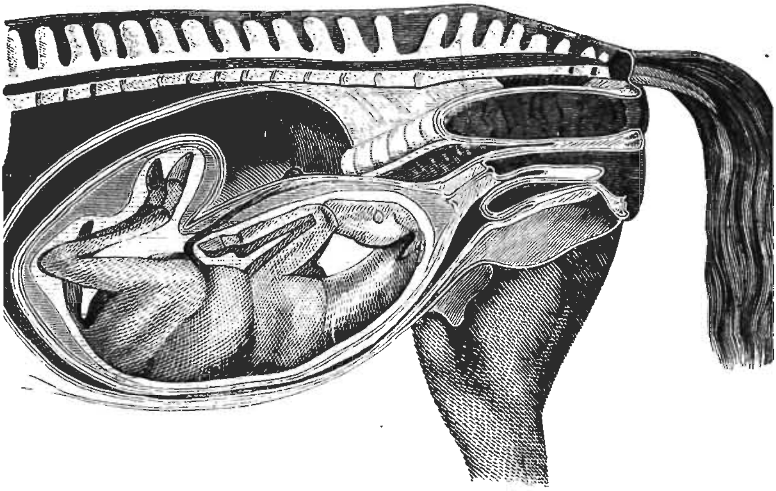


Fig. 97. Normal position of foal before parturition (after Franck, from Fleming, Messrs Baillière, Tindall and Cox).

It begins almost immediately after conception but is not pronounced until after two or three months in the mare or cow. In animals which have previously been pregnant the change is not very apparent until shortly before parturition. In the last weeks a serous fluid can be expressed from the teats and as parturition approaches this fluid becomes more and more opaque and milk-like. In lactating mares and cows the milk supply diminishes and the animal 'dries off' as a new pregnancy proceeds, there being little or no secretion from about the seventh or eighth month in the mare or the sixth or seventh month in the milch cow until the new supply begins in the final stages of pregnancy.

Parturition. During uterine life the young foal, calf or lamb

lie on their backs within the uterus on the floor of the mother's abdomen, but shortly before birth the foetus turns on its side taking a lateral position, and then turns still further assuming an upright position. The foetus is then brought into a position in which the muzzle rests upon the fore legs, these being extended in the direction of the vaginal opening, while the hind limbs are drawn up under its body. This method of presentation (anterior or 'head presentation') is the most normal, but it often happens that the hind legs appear first (posterior or 'breach presentation') or the foetus may be presented transversely or cross-wise.

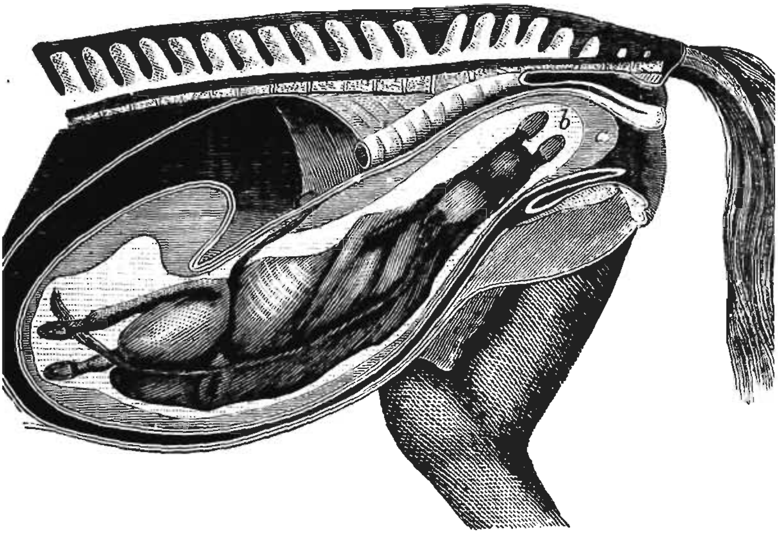


Fig. 98. Second position preparatory to parturition (after Franck from Fleming. Messrs Baillière, Tindall and Cox). *a* amnion, *b* allantois.

The mother as the time for parturition draws near becomes increasingly disturbed and restless, frequently changing her position. When the actual 'pains' commence she shows evident signs of distress, and the skin becomes hot and the pulse rate rapid, but each 'pain' is succeeded by an interval of calm.

The 'pains' are caused by the contraction of the longitudinal muscles of the uterus which in this way dilate the os or mouth of the uterus. Even in the virgin the uterine muscles undergo very slight rhythmic contractions as may be seen when the organ is withdrawn from the body and kept in salt solution at body temperature, and these contractions may be greatly increased by applying

mechanical stimuli. During the anoestrum the uterine contractions are always very slight and infrequent, and it is only during pregnancy and with the approach of parturition that they become considerable. At such times, as already mentioned, the muscles of the uterus are very greatly developed.

The dilatation of the os marks the first stage of labour. In the second stage all the uterine muscles contract, as well as those of the abdominal wall and the diaphragm. These coordinated muscular movements expel the foetus from the uterus to the vagina, and thence to the exterior, the final propulsion from the

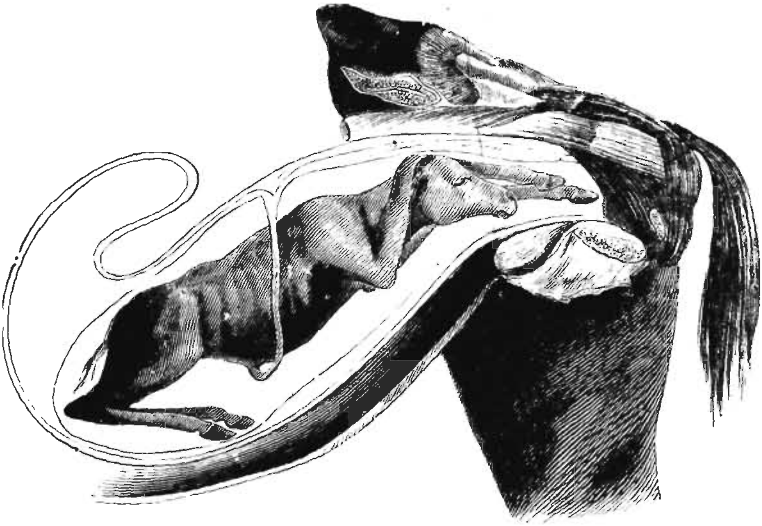


Fig. 99. Third position preparatory to parturition (after Franck, from Fleming, Messrs Baillière, Tindall and Cox).

vagina being due chiefly to the contractions of the abdominal muscles. The foetal membranes which contain fluids and serve as a sort of elastic bag round the young animal, thus protecting it from mechanical shock or jar, are the first to appear. The 'water bag' then ruptures, some of the fluid escaping, and the young animal soon afterwards makes its appearance.

The third stage of parturition consists of the expulsion of the foetal membranes which together constitute the afterbirth. This is done by further contractions of the uterine muscles accompanied by the action of the diaphragm and muscles of the abdomen. Sometimes, as not infrequently happens in the mare, the young

animal is born within the intact membranes and should be liberated in order to avoid asphyxiation, but more usually a few minutes or more elapse before the placenta is detached and got rid of. Occasionally the membranes are retained in the uterus where they are liable to become infected with bacteria and set up inflammation; if they are not discharged steps should be taken to remove them.

The duration of parturition varies in the different species. In the mare it takes from 5 to 15 minutes, in the cow about two hours, in the sheep 15 minutes for each lamb born, in the sow, bitch and cat from 10 to 30 minutes with sometimes an interval of one hour between each birth. In the Carnivora, the mother usually gnaws through the umbilical cord, but in the other

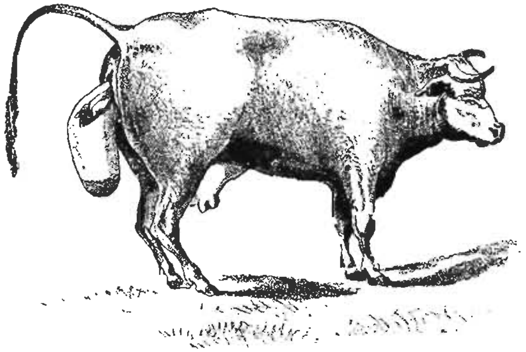


Fig. 100. Cow in act of calving (after Fleming, Messrs Baillière, Tindall and Cox).

animals it is torn. The afterbirth may not be got rid of until several hours after the young is born (as in the mare).

The normal process of parturition depends upon the integrity of the spinal cord which coordinates the various muscular movements, but as already mentioned the uterus undergoes rhythmical contractions independently of its nerve connections and will do so after separation from the body if maintained at the normal temperature and suspended in a suitable saline fluid. Goltz has shown that the bitch will give birth to pups after the complete exsection of the spinal cord in the lumbo-sacral region, and Simpson in an experiment on the sow in which the posterior spinal cord was destroyed showed that a litter of young pigs could be expelled by uterine action alone, excepting for the last pigling which remained in the vagina owing to the abdominal muscles

not acting and there being no young ones in process of passing out from the uterus to propel the last pigling through the vaginal opening.

Abortion or premature parturition may occur at any time during gestation. There are two kinds, sporadic and contagious abortion. The former may occur as a result of undue muscular exertion, fatigue, injury, excitement or fright, or it may be caused by illness (e.g. digestive trouble or the taking of frozen food) or by eating ergot or other substances which act upon the uterine muscles. Contagious abortion is due to a bacillus and is especially common in cattle; it may be transmitted by the bull or the contagion may be spread through contaminated litter, the bacilli probably entering through the vagina and passing into the uterus. Immunity, at any rate for a certain period, is acquired through an attack. Contagious abortion also occurs in mares, and occasionally in sheep and pigs but is due usually to different organisms which are in some degree specific for the animals attacked.

Lactation. The mammary glands which have been already described, commence to secrete at or shortly before parturition, the thin colostrum which at first appears rapidly giving place to true milk. The capacity for milk production varies widely in the different breeds, some cows going on yielding until the approach of a new parturition before going dry. The drawing off of milk is itself a factor in the yield, since as is well known, a 'quarter' will go dry if the milk secreted is not removed by milking or sucking; in such cases the milk constituents are reabsorbed and lactose may often be found in the urine. The physiological factors in the growth of the glands and the secretion of the fluid are referred to below in dealing with the ovarian secretions.

Fecundity. The number of young produced at a litter is dependent primarily upon the number of ova discharged at ovulation which occurs during oestrus. With the mare and cow this number is generally one, but double and even triple births are not unknown. With the ewe one or two young are born at a time, while triplets are not uncommon, and four or five lambs have occasionally been produced at one time. The sow may give birth to any number up to 16, and occasionally more, a litter of 24 having been recorded. The bitch has been known to produce as many as 23 pups, but any number higher than 12 is very rare; an

average sized litter consisting of four or five pups while the number is often fewer.

The number of lambs produced may be increased by the process of 'flushing' the ewes, that is, by giving them extra feeding, cake, corn or turnips for a few weeks before tupping time, this practice not merely increasing the number of ripe follicles available for ovulation at any one time, but also having the effect of hastening forward the sexual season. After tupping is over extra feeding is no longer of use in increasing fecundity since the number of developing young has already been determined.

It is clear that, speaking generally, the female is a more important factor than the male, since whereas the number of ripe ova available for fertilisation is very limited, the number of spermatozoa entering the female passages is excessive.

In the sow Hammond has shown that whereas a very large number of ova may be fertilised, some of these may only undergo a very limited degree of development, but it is uncertain what precise factors are responsible for this failure. It is possible that some of the ova possess an insufficient vitality from the outset, and this may possibly be the result of inbreeding which is believed to tend towards infertility. Thus Heape states that Dorset Horn ewes will sometimes produce lambs when put to Hampshire Down rams but will not breed when served by rams of their own variety. It is possible that the fertilised ovum is endowed with a superior vitality by having conjugated with a spermatozoon belonging to a different breed.

Fertility like other characteristics can be inherited, and a ram which was one of twins and consequently of fertile stock may transmit this capacity to female progeny. It is improbable, however, in view of what has been said above, that the male parent can generally be responsible for the size of the litters produced by the females served by him. Nevertheless fertility may be transmitted through the male in just the same way as the milking capacity of a dairy cow may be transmitted through the male progeny to the next generation of females.

The reproductive period in the life of the female begins at puberty when the generative organs develop, the first batch of ova become mature, and the first oestrous cycle commences: it ends at the menopause or climacteric when the generative organs become atrophic and the cycle closes. The mare begins to breed

in her second year, puberty generally occurring at about 16 to 18 months. Heifers take the bull at 12 to 14 months but may experience puberty earlier. The sow may take the boar at 4 or 5 months but puberty is generally later. Ewe lambs dropped in the spring may breed in the following autumn. Bitches and cats experience puberty at 8 to 10 months, sometimes later, and occasionally earlier. The time when reproduction ceases is very variable and in practice most domestice animals die long before they reach their menopause. Mares have bred even at 30 years and ewes at 21, but such cases are very exceptional.

Fig. 101. Lonk sheep aged 18 years with her last lamb This sheep which belonged to Mr William Peel of Knowlemere Manor, Clitheroe lived to be 21 after having 35 lambs, nine of which were triplets. (From Marshall.) From photograph supplied by Lieut.-Col. W. R. Peel.

The Internal Ovarian Secretions. In addition to the oogenetic function the ovaries are organs of internal secretion, and through these exercise an influence over the female metabolism comparable to that possessed by the testes in the male. In birds removal or atrophy of the ovaries tends towards the assumption of certain of the male characters. Thus in female poultry there is apt to be a development of the spurs, hackles and feathering of the cock, and it is well known that old hens which have ceased to lay often take to crowing. The relation between the ovaries and

the external characters of the sex is however very obscure, and in mammals removal of the ovaries does not lead to the development of male characters (e.g. in Herdwick sheep which are horned in the male but hornless in the female, ovariotomy or extirpation of the ovaries does not lead to horn development).

That the ovaries are responsible for the oestrous cycle is

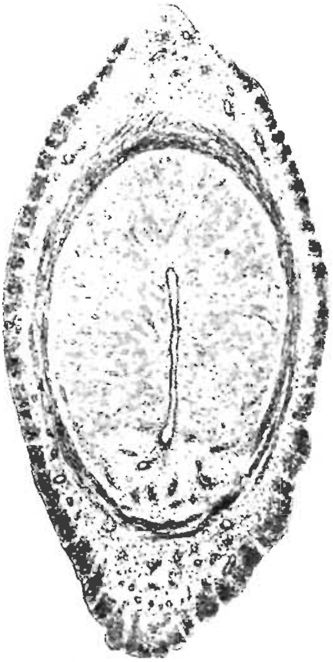


Fig. 102. Transverse section through uterus of rat, six months after ovariotomy, showing degenerative changes (from Marshall).

certain, for ovariotomy is followed by atrophy of the uterus and heat no longer recurs. That the ovarian influence is chemical rather than nervous is proved by the fact that successful transplantation of the ovaries to an abnormal position, such as on to the ventral wall of the body cavity or into the tissue of the kidney, is sufficient to admit of the recurrence of the cycle and the normal maintenance of the uterine nutrition in spite of the ordinary nerve connections of the ovaries having been severed. The grafted

ovaries are capable of producing ripe ova, and ovulation may occur, followed by the formation of typical corpora lutea.

At the prooestrous and oestrous periods when the ovaries are in a state of enhanced activity as manifested especially by the growth and maturation of the Graafian follicles, the uterus also becomes active, undergoing growth and congestion and the other

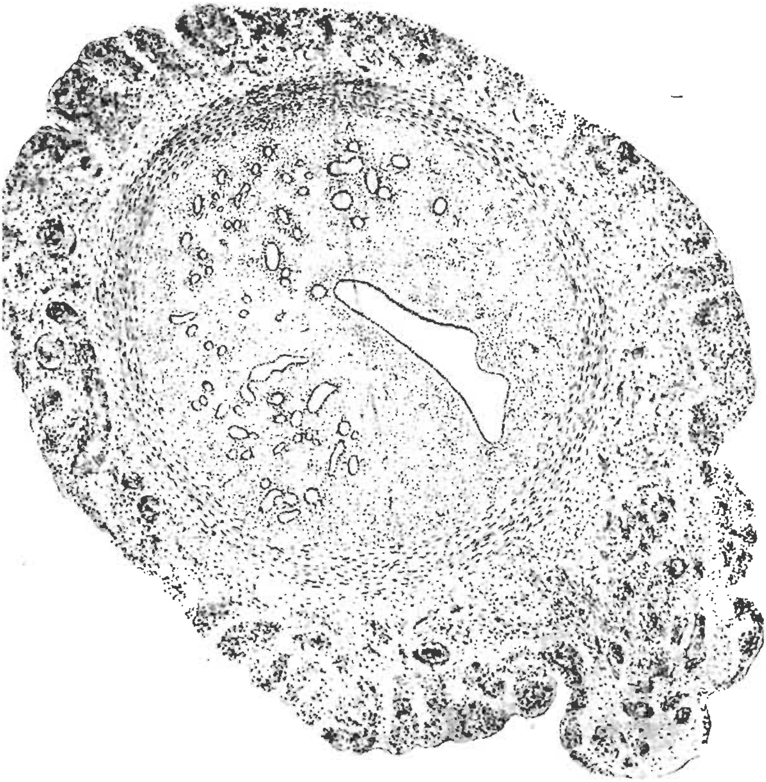


Fig. 103. Transverse section through uterus of rat six months after transplantation of ovary to ventral wall of peritoneum. The uterus is normal. (From Marshall.)

changes characteristic of heat, as already described. Furthermore, the mammary glands become slightly swollen. It is not however until a later period when the corpora lutea are formed in the ovaries that the uterine mucous membrane undergoes the pronounced hypertrophy characteristic of pregnancy or pseudo-pregnancy. The mammary glands develop during the same period. More-

over it has been established that these developmental changes both uterine and mammary, do not occur in the absence of corpor lutea, as when ovulation had not taken place at oestrus. Experiments have proved clearly that both the uterine growth and th mammary growth are dependent upon the presence of lutea

Fig. 101. Transplanted ovary of rat, showing corpora lutea, and small follicle (from Marshall).

tissue in the ovaries, and under the influence of the corpora lute the mammary glands develop to an extent sufficient to admit o milk production at and after parturition or at a correspondin period at the end of pseudo-pregnancy. In polyoestrous animals

the corpora lutea, if pregnancy does not occur, usually degenerate after a short interval and before another heat period is due, since

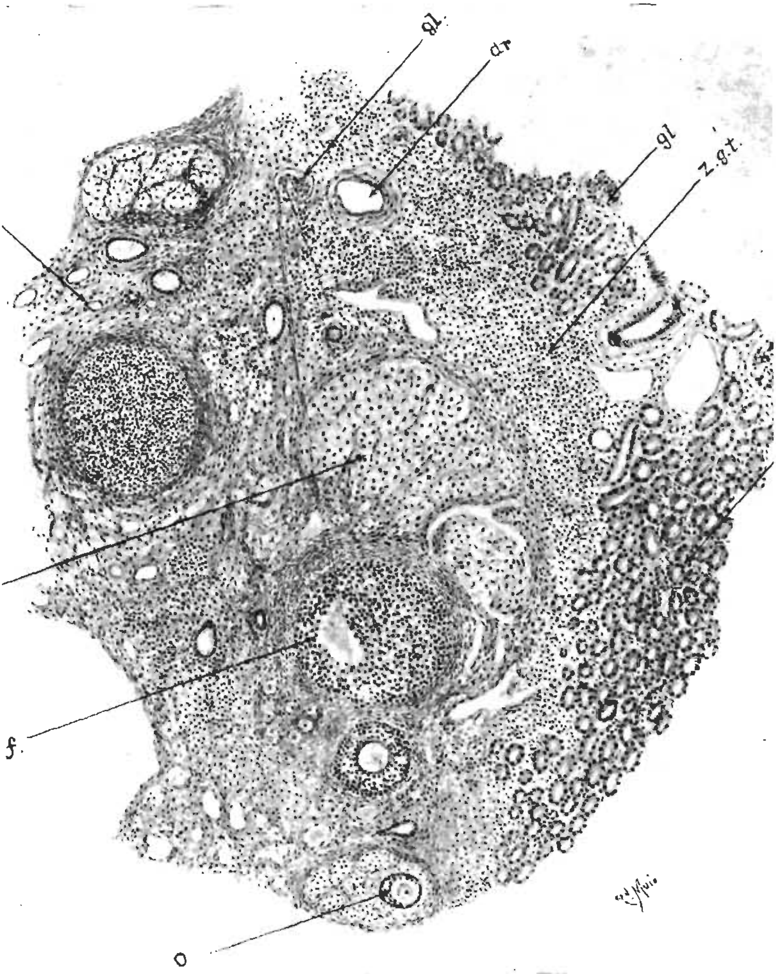


Fig. 105. Section through rat's kidney into which ovary has been transplanted. *ar.* artery, *c.l.* corpus luteum, *g.f.* Graafian follicle, *gl.* glomerulus of kidney, *o.* ovum, *ov. st.* ovarian stroma, *r.t.* renal tubule, *z.g.t.* zone between ovarian and renal tissue.

the presence of these organs in the ovaries has an inhibitory influence upon follicular development and upon the occurrence of oestrus.

In view of these and other facts it seems certain that the ovaries are organs elaborating internal secretions which change both in character and quantity during the successive phases of the oestrous cycle, and that these secretions are responsible for the various processes which recur rhythmically in the uterus and mammary glands. During the anoestrum the ovarian secretions suffice to preserve the normal nutrition of the uterus and to prevent that organ from lapsing into the infantile condition. During the prooestrum and oestrus they stimulate the uterine and mammary tissues to undergo some amount of growth. But it is not until the corpus luteum is formed that the ovary acquires its maximum influence upon the accessory generative organs and mammary glands which then undergo the extensive anabolic changes without which the young could not obtain the nourishment which is necessary for their growth and development.

Schafer and others have shown that extracts of corpus luteum and posterior lobe of pituitary during lactation have a galactogogue influence upon the mammary glands causing an instant and copious secretion of milk. These observations further emphasise the functional connection between these organs and the milk glands, but it is possible that the sudden injection of these extracts in considerable quantity has a somewhat different and more violent effect than the slow passage of the problematical hormones into the circulation, such as one may presume to occur in nature. Moreover it may be that this building up of the mammary tissues is a process not essentially different from that concerned in milk secretion but that the two phenomena are in reality parts of a process of the same nature throughout (that is to say, it is not necessary to regard them as representing two opposing tendencies, one anabolic and the other katabolic)[1].

It is known that double ovariotomy results in the hypertrophy of the pituitary gland, and also that double ovariotomy during lactation leads to almost indefinite continuation of milk secretion, and it seems not improbable that these two facts are connected. Furthermore, it is conceivable that the hypertrophied pituitary compensates for the absence of the corpus luteum, and that unlike the latter organ, persists for a very extended period

[1] Apart however from these factors the removal of the secretion in sucking or milking is necessary for continued lactation, and a cow whose milk is not withdrawn very soon becomes dry.

during which it exercises a stimulating influence over the mammary tissue.

Ovariotomy or spaying is practised on the sow in order to promote growth or fattening but this is only done in some parts of the country and by no means habitually. It has been fairly established however that when the operation is done properly the results are commercially profitable. Faulty spaying in which ovarian tissue is left behind has helped to discredit the practice, and this result has been unfortunate. The sows should be operated on at about seven weeks old or the same age as that at which the males are castrated. Hobday recommends ovariotomy for troublesome mares to render them easy to work during oestrus and has obtained some useful results. Ovariotomy is only very rarely performed on the cow but when done during lactation leads to long-continued milk secretion as just mentioned.

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